CHELICERAL MORPHOLOGY IN SOLIFUGAE (ARACHNIDA): PRIMARY HOMOLOGY, TERMINOLOGY, AND CHARACTER SURVEY

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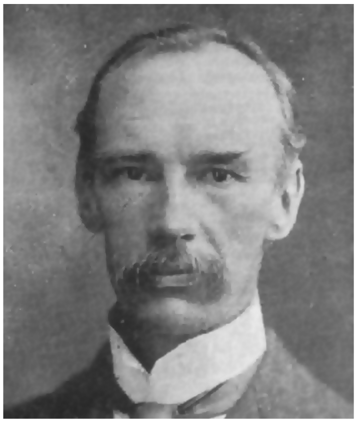
Karl M. F. M. Kraepelin
(1848–1915)



Reginald I. Pocock
(1863–1947)

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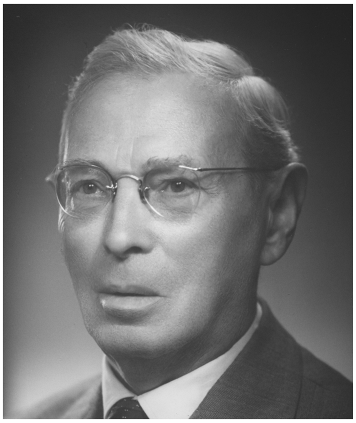

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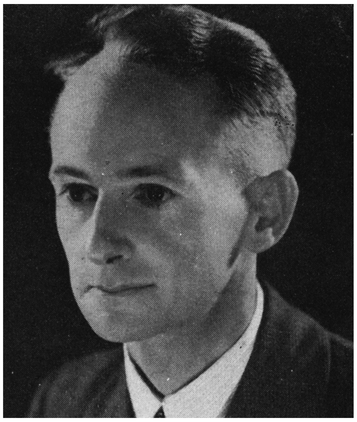

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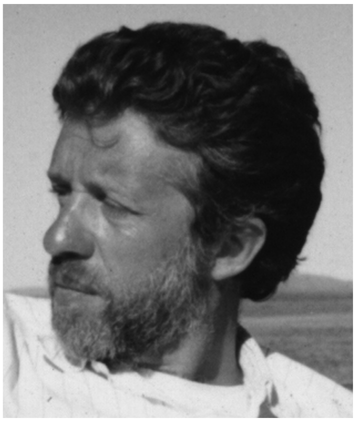

Emilio A. Maury
(1940–1998)

Some of the most prominent workers on Solifugae from the past two centuries: Karl M. F. M. Kraepelin (Germany); Reginald I. Pocock (United Kingdom); Alexei A. Byalynitsky-Birula [A. A. Birula] (Russia); William F. Purcell (South Africa); John Hewitt (South Africa); Carl F. Roewer (Germany); Reginald F. Lawrence (South Africa); Martin H. Muma (U.S.A.); Emilio A. Maury (Argentina).

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ABSTRACT

Arachnids of the order Solifugae (solifuges, false spiders, sun spiders, camel spiders, *Walzenspinne,* wind spiders) possess the largest jaws for body size among the Chelicerata. The chelicerae provide the most important character systems for solifuge systematics, including dentition and the male cheliceral flagellum, both used extensively for species delimitation and diagnosis. However, the terminology used for cheliceral characters is not standardized and often contradictory, in part because it fails to represent homologous structures among taxa. Misinterpretation of character homology may introduce errors in phylogenetic analyses concerning relationships within Solifugae and among the orders of Chelicerata. This contribution presents the first comprehensive analysis of cheliceral morphology across the order Solifugae, the aims of which were to provide a broad survey of cheliceral characters for solifuge systematics, to identify and reinterpret structures based on primary homology, to revise the terminology to be consistent with homology hypotheses, and to provide a guide to terminological synonyms and character interpretations in the literature. Chelicerae were studied in 188 exemplar species (17% of the total), representing all 12 solifuge families, 17 of the 19 subfamilies, 64 genera (46% of the total), and the full range of variation in cheliceral morphology across the order. In total, 157 species representing 49 genera and 17 subfamilies are illustrated. Hypotheses of character transformation, particularly concerning the male flagellum, and a standardized terminology, are presented. The functional morphology of the chelicerae is discussed and the role of sexually dimorphic modifications to the male chelicerae in mating behavior emphasized. The revised terminology, based on hypotheses of primary homology, will facilitate solifuge revisionary systematics and provide a stronger basis for reconstructing phylogenetic relationships within the order Solifugae and testing the phylogenetic position of the order within Chelicerata.

Keywords: Chelicerata, chaetotaxy, dentition, functional morphology, male flagellum, mating, stridulatory apparatus, comparative morphology, homology, terminology

INTRODUCTION

The Solifugae (fig. 1) are a relatively poorly known order of arachnids (Harvey, 2002b), also known as solifuges, solifugids, solpugids, and various other vernacular names describing either the order or specific families or genera within it, e.g., *baardskeerders,* camel spiders, false spiders, *haarskeerders, jaag-* or *jagspinnekoppe,* jerrymanders, red romans, roman spiders, sun spiders (or sun scorpions), *Walzenspinnen,* wind spiders (or wind scorpions). This mesodiverse order currently comprises 12 extant families, 139 genera, and 1105 species (Harvey, 2003; Prendini, 2011; see section on Taxonomic Overview). Although the phylogenetic placement of Solifugae within Chelicerata remains unresolved (e.g., Alberti and Peretti, 2002; Dabert et al., 2010; Pepato et al., 2010; Sharma et al., 2014), morphological and molecular analyses have repeatedly confirmed the monophyly of the order (e.g., Hayashi et al., 1992; Wheeler and Hayashi, 1998; Giribet et al., 2002; Shultz, 2007; Giribet and Edgecombe, 2012).

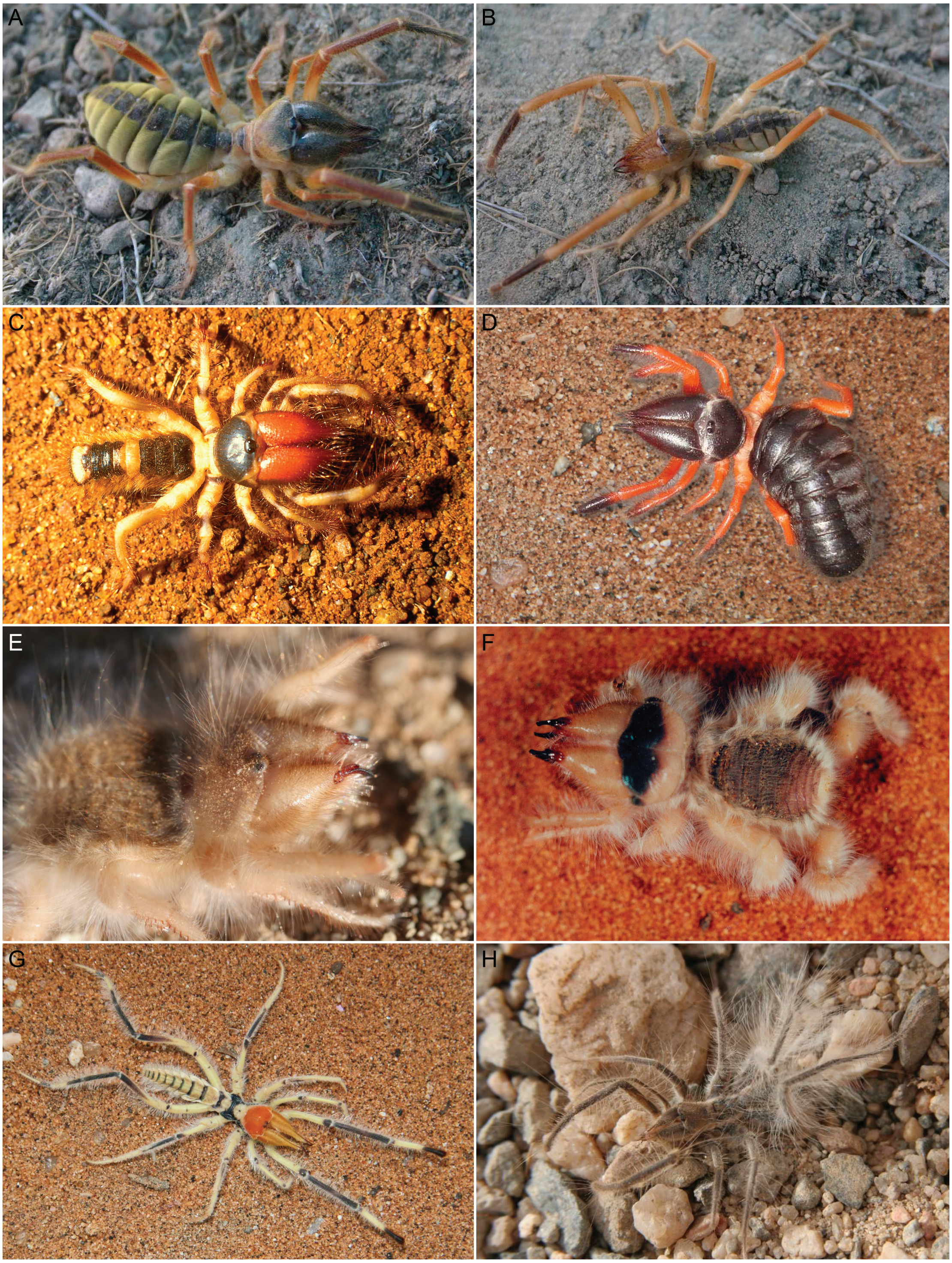
The most comprehensive treatment of Solifugae to date was the work of Roewer (1932–1934), who summarized most of the available literature, and added many new observations and interpretations of solifuge morphology. Nearly eight decades on, Roewer (1932–1934) remains the primary citation for solifuge morphology. For example, Shultz (2007) cites Roewer (1934) 16 times as a source of information for coding solifuge characters in his study on chelicerate phylogeny, 14 as the sole citation.

Roewer (1932, 1933, 1934, 1941, 1942, 1952a, 1952b, 1952c, 1954a, 1954b, 1954c, 1954d, 1957, 1960, 1961) laid the foundation of the modern classification of Solifugae, but was extensively criticized for emphasizing characters, especially leg “spination” and cheliceral dentition, which are “variable” (Birula, 1936b; Panouse, 1950, 1961a, 1961b; Muma, 1951, 1976; Lawrence, 1955, 1976; Turk, 1960; Simonetta and Delle Cave, 1968; Wharton, 1981; Gromov, 2000, 2003a; Harvey, 2002b, 2003), even on individual specimens (e.g., Panouse, 1961a, 1961b). However, there remains little evaluation and quantification of both intra- and interspecific variation in Solifugae. Roewer’s (1934) classification, described as “confusing” and “chaotic” (Vachon, 1950: 107; Turk, 1960: 106), was refined by Muma (1976), who placed greater emphasis on male secondary sexual characters, particularly the cheliceral flagellum (**male flagellum**), cheliceral dentition, and associated structures, but his work likewise remained devoid of phylogenetic content (Harvey, 2002b, 2003). No subordinal or suprafamilial groupings exist. Several families and many genera are unlikely to be monophyletic. Subfamilial groupings have been criticized as superficial (e.g., Lawrence, 1953; Muma, 1976; Wharton, 1981). Except for one work on the New World *scaber* group of *Eremobates* Banks, 1900 (Brookhart and Cushing, 2004), no phylogenetic analyses have been published on solifuges and comprehensive revisionary syntheses are lacking for most families and genera.

The absence of a phylogenetic framework for Solifugae may, in large part, be attributed to the absence of a unified synthesis of homologous characters across the order. Related to this is the absence of standardized terminology. Characters proposed by Roewer (1934) were adopted by some solifuge workers, but not others, often without clear definitions, resulting in an inconsistent assortment of terms and interpretations across the solifuge literature. No attempt has been made to homologize structures across Solifugae and base terminology thereon, with few exceptions, e.g., some noncheliceral terminologies based on homology assessments between Solifugae and other chelicerate orders (Dunlop, 2000, 2002; Dunlop et al., 2012). Harvey’s (2002b: 366) statement that “[m]uch work must be undertaken to even begin to sort out the confusion” in Solifugae taxonomy is equally applicable to solifuge morphology, which requires precise, standardized terms, based on hypotheses of homology, to facilitate communication.

Early on, Dufour (1861: 344) stressed the importance of comparing structures before promoting terms in solifuge morphology. Indeed, efforts to base standardized terminology on hypotheses of homology are common in biology, but with various levels of acceptance depending on the extent to which the terms to be replaced are established in the literature. For example, Snodgrass (1948) proposed new terminology for the mouthparts of Acari, based on careful investigations of mouthpart homology across arachnids (including terms recently promoted for the Solifugae rostrum; see Dunlop, 2000), which was largely ignored by acarologists, because a relatively standardized terminology was already in place. Given the inconsistency in solifuge morphological terminology, and the resurgence in solifuge research (e.g., Ballesteros and Francke, 2007; Reddick, 2008; Catenazzi et al., 2009; Klann, 2009; Carvalho et al., 2010; Erdek, 2010, 2015; Reddick et al., 2010; Bayram et al., 2011; Conrad and Cushing, 2011; Valdivia et al., 2011; Willemart et al., 2011; Cushing and Castro, 2012; Dunlop and Klann, 2009; Dunlop et al., 2012; Yiğit et al., 2012; González Reyes and Corronca, 2013; Karataş and Uçak, 2013; Cushing et al., 2014; Botero-Trujillo, 2014; Iuri et al., 2014; Wharton and Reddick, 2014), it is an opportune time to unify and redefine solifuge morphological terminology in light of modern concepts of character homology, advances in technology, and the availability of new material.

The present contribution is concerned with characters of the **chelicerae** of Solifugae, which bear the greatest concentration and arguably the most important characters for solifuge systematics, from species delimitation to phylogenetic reconstruction (Kraepelin, 1908a; Hewitt, 1919b; Cloudsley-Thompson, 1984: 195). The aims of the project were as follows: (1) survey external cheliceral characters across a broad selection of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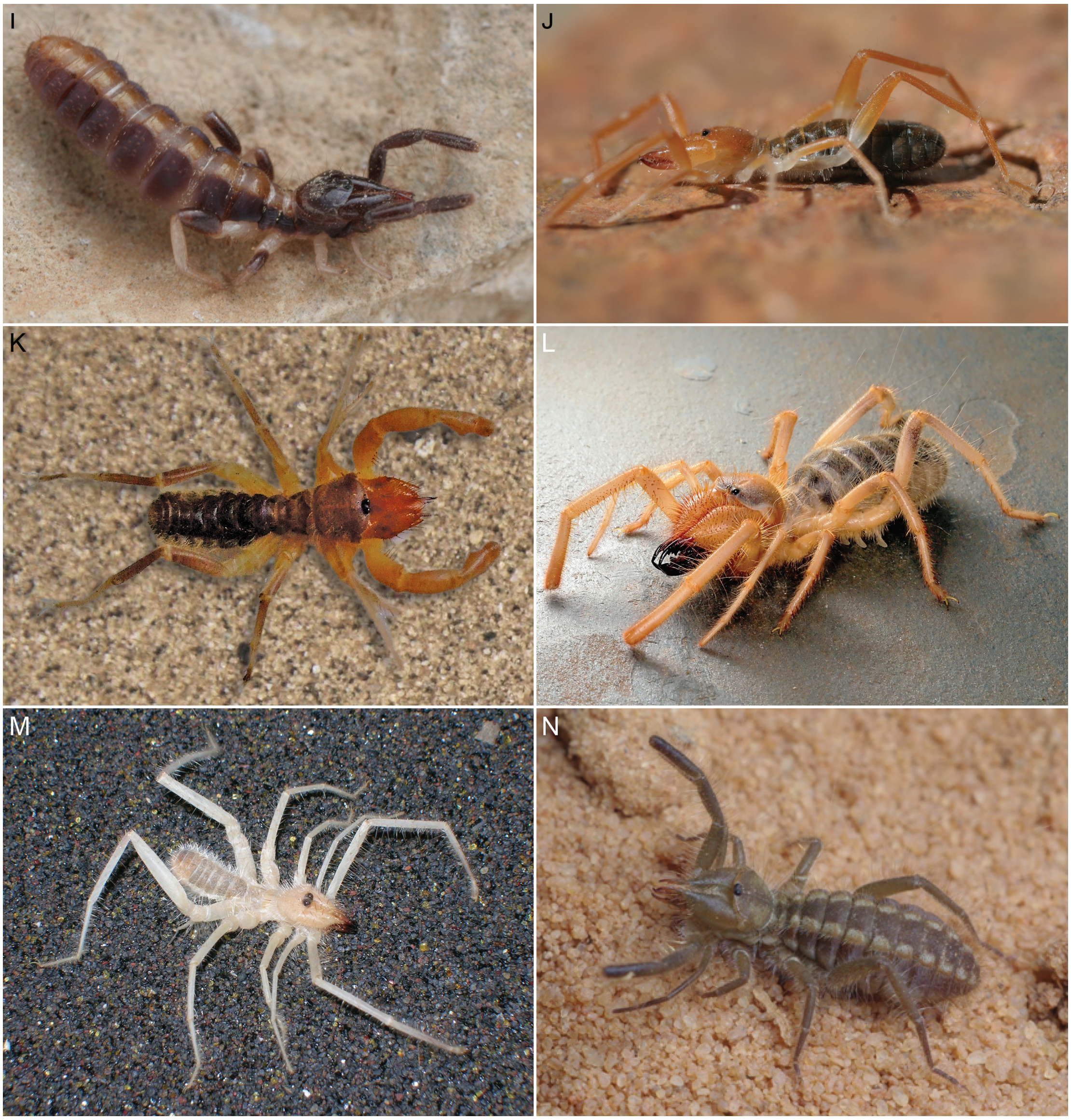

FIG. 1. Galeodidae Sundevall, 1833 (**A, B**), Rhagodidae Pocock, 1897 (**C, D**), Hexisopodidae Pocock, 1897 (**E, F**), Solpugidae Leach, 1815 (**G, H**), Daesiidae Kraepelin, 1899 (**I, J**), Gylippinae Roewer, 1933 (**K**), Eremobatidae Kraepelin, 1899 (**L**), Ammotrechidae Roewer, 1934 (**M**), and Mummuciidae Roewer, 1934 (**N**), habitus in life. **A, B** *Galeodes caspius fuscus* Birula, 1890, Kazakhstan, ♀ (**A**) and ♂ (**B**). **C.** *Rhagodes* sp., ♀, Kenya. **D.** *Rhagodes* sp., ♀, India. **E.** *Hexisopus* sp., ♀, Namibia. **F.** *Chelypus* sp., ♂, Namibia. **G.** *Metasopuga picta* (Kraepelin, 1899), ♂, Namibia. **H.** *Zeria sericea* (Pocock, 1897), ♂, Namibia. **I.** *Hemiblossia* sp., ♀, Namibia. **J.** *Blossia* sp., ♂, Namibia. **K.** *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂, Turkey. **L.** *Eremocosta striata* (Putnam 1883), ♀, U.S.A. **M.** *Nothopuga cuyana* Maury, 1976, ♂, Argentina, **N.** *Gaucha* sp. ♀, Brazil.

TABLE 1

Mode of sperm transfer in families of Solifugae for which data available

Based on Heymons (1902), Cloudsley-Thompson (1961, 1967a, 1967b), Amitai et al. (1962), Junqua (1962), Muma (1966b), Wharton (1987), Punzo (1998b), Peretti and Willemart (2007), and Hrušková-Martišová et al. (2010a).

	Direct sperm transfer	Flagellum	Cheliceral finger(s)
Ammotrechidae Roewer, 1934		x	
Daesiidae Kraepelin, 1899			x
Eremobatidae Kraepelin, 1901	x		
Galeodidae Sundevall, 1833			x
Solpugidae Leach, 1815			x

exemplar species, representing the taxonomic and morphological diversity of the order; (2) evaluate variation in characters or character systems within and among solifuge taxa to determine their utility for systematics; (3) propose hypotheses of primary homology across the order; (4) present a precise, standardized, and unambiguous terminology, reflecting the hypothesized homology of structures; (5) provide a guide to terminological synonyms and character interpretations in the literature; (6) identify potential synapomorphies for taxa (with an emphasis on the family level but extending to the genus level); and (7) discuss the functional morphology of the chelicerae and their components.

Importance of Chelicerae in Solifugae

The chelicerae are the first pair of appendages on the prosoma of Chelicerata (Snodgrass, 1928: 30; Manton, 1977: 239). Their homology with "head" structures in other arthropod taxa has long been debated. The chelicerae of solifuges were variously interpreted as structures without any counterpart in insects (Savigny, 1809: 176), as homologous to the antennae (Latreille, 1829) or mandibles (e.g., Blanchard, 1847: 233) of insects, or as homologous to the first (Viallanes, 1892) or second (Latreille, 1829) pair of antennae of crustaceans. Snodgrass (1965), like Petrunkevitch (1913) before him, homologized the solifuge chelicera with the second antennae of Crustacea, and with the putatively lost intercalary segment of insects. Latreille (1829: 207) was the first to homologize the chelicerae with mandibulate antennae, and introduced the terms *chelicerae* (Greek, *chele*, claw; *keras*, horn) or *antenne-pinces*. This view (for a more detailed summary of historical literature, see Riley, 1902) came full circle with recent evolutionary developmental studies, which confirmed the homology of chelicerae, mandibulate antennae, and the first antennae (antennules) of crustaceans (e.g., Giribet and Edgecombe, 2012), initially supported by deutocerebral innervation (Mittmann and Scholtz, 2003) and the absence of Hox gene expression in the cheliceral/antennal segment (Telford and Thomas, 1998), and later by similarities in the expression of genes that pattern the proximodistal axis of these appendages (Sharma et al., 2012).

Solifuges are easily distinguished from other arachnids by their massive two-segmented, chelate chelicerae (pl. 1), usually bearing a flagellum in the adult male. Solifuge chelicerae are the largest per body size within Chelicerata (Roewer, 1934: 52), rivaled only by those of basal pseudoscorpions in the superfamilies Chthonioidea and Neobisioidea (Chamberlin, 1931; Shultz, 1990). The chelicerae perform a greater diversity of functions in Solifugae than in any other chelicerate order. Solifuges use the chelicerae for prey capture and feeding (Muma, 1966c; Wharton, 1987; Cloudsley-Thompson, 1977a), fighting with conspecifics (Muma, 1967), defense, burrowing (Muma, 1966a; Cloudsley-Thompson, 1977a), and mating (Heymons, 1902; Cloudsley-Thompson, 1961, 1967a, 1967b; Amitai et al.,

TABLE 2

Reproductive behavior associated with cheliceral structures of male Solifugae

Based on observations of species in five families: Ammotrechidae Roewer, 1934: *Oltacola chacoensis* Roewer, 1934, in Peretti and Willemart (2007); Daesiidae Kraepelin, 1899: *Gluvia dorsalis* (Latreille, 1817), in Hrušková-Martišová et al. (2010a); Eremobatidae Kraepelin, 1901: *Eremobates durangonus* Roewer, 1934, *E. nodularis* Muma, 1951, and *E. palpisetulosus* Fichter, 1941, in Muma (1966b), and *E. marathoni* Muma, 1951, in Punzo (1998b); Galeodidae Sundevall, 1833: *Galeodes caspius* Birula, 1890, in Heymons (1902), *G. caspius subfuscus* Birula, 1937, in Hrušková-Martišová et al. (2008a, 2010a), *G. granti* Pocock, 1903 (misidentified as *G. arabs*), in Cloudsley-Thompson (1961, 1967a, 1967b), *G. sulfuripes* Roewer, 1934, in Amitai et al. (1962), and *Othoes saharae* Panouse, 1960, in Junqua (1962); Solpugidae Leach, 1815: *Metasolpuga picta* (Kraepelin, 1899) in Wharton (1987).

Abbreviations: **FF,** fixed finger; **GP,** gonopore; **MF,** movable finger.

Phase		Dentition, mucron	Chelicera	Fixed finger	Dorsal macrosetae	Flagellum
Somatic contact	initial grabbing of ♀	grasp, bite, pinch opisthosoma, legs, peltidia				
	somatic massage	chew opisthosoma, propeltidium, chelicerae (lightly or fiercely)				
	move ♀	lift, run with ♀; drag ♀ by GP up vertical surface				
Genital contact[a]	preinsemination	knead, pinch, chew ♀ operculum, surrounds; FF into ♀ GP, grip opisthosoma with MF	thrust chelicera in, out of GP	FF into GP	press setae against genital region	
	insemination	collect/lift, chew sperm droplet; open opercula; insert sperm		insert FF into GP		place sperm in flagellum, insert into GP (Ammotrechidae)[b]
	postinsemination	prod GP with tips of fingers	insert chelicera deeply into, or in, out of GP		press dorsal chelicera against ♀ genital area (Galeodidae)	insert flagellum fully into ♀ genitalia (Solpugidae)[c]
Release		pinch sides of GP opening together				close GP (Galeodidae)[d]

[a] Genital contact phase, especially pre- and postinsemination actions generally violent, described using phrases such as "deeply inserted [cheliceral fingers]…rub intensely" (Hrušková-Martišová et al., 2010a: 95) and *großer Gewalttätigkeit* "[great violence/vigorous]" (Heymons, 1902: 42); exceptions during insemination phase described using phrases such as "gently" (Cloudsley-Thompson, 1961: 160) and "inserted cheliceral tips" (Wharton, 1987: 376).

[b] The male *O. chacoensis* picked up the sperm with the tarsi of his first pair of legs, placed it "between the [spoonlike] flagella," and inserted finger and flagellum into the female genital tract (Peretti and Willemart, 2007: 34).

[c] The male *M. picta* inserted flagellum and chelicera into the female genital tract, with the flagellar shaft held at an angle of 45–90° relative to its normal resting position (Wharton, 1987). The flagellum was completely inserted into the female; the tip glistened on removal (R.A. Wharton, personal obs.).

[d] The genital opening of the female *G. caspius subfuscus* was closed as follows: "using two cheliceral fingers and flagella, [the male] gripped the soft cuticle of the female's opisthosoma and pulled it toward the operculum" (Hrušková-Martišová et al., 2010a: 95). It is unclear how the flagellum was involved.

TABLE 3

Sperm packaging in families of Solifugae for which data available

Based on Klann et al. (2009, 2011); also see Warren (1939), and Klann (2009). Note that aggregations of spermatozoa should not be confused with spermatophores, i.e., sperm packages, which are formed by secretions of the accessory glands (Klann et al., 2009). According to this definition, spermatophores have not been observed in Solifugae (Warren, 1939; Klann, 2009; Klann et al., 2011) and references to spermatophores in solifuges (e.g., Kaestner, 1933; Cloudsley-Thompson, 1961; Wharton, 1987) probably refer to the viscous sperm mass (Klann et al., 2009).

	Single cells[a]	Groups of cells[b]	Cleistospermia[c]	Coenospermia[d]
Ammotrechidae Roewer, 1934		x		
Daesiidae Kraepelin, 1899	x (*Biton* Karsch, 1880)			x (*Blossia* Simon, 1880)
Eremobatidae Kraepelin, 1901	x			
Galeodidae Sundevall, 1833				x
Hexisopodidae Pocock, 1897			x	
Karschiidae Kraepelin, 1899		x		
Solpugidae Leach, 1815	x			

[a] Spermatozoa remain as single cells.

[b] Spermatozoa clumped together into groups of loose-knit (Ammotrechidae) or highly ordered (Karschiidae) cells.

[c] Individual spermatozoa surrounded by thin secretion sheath.

[d] Several sperm cells surrounded by thick (Galeodidae) or thin (*Blossia*) secretion sheath in testis or vasa differentia.

1962; Junqua, 1962; Muma, 1966b; Wharton, 1987; Punzo, 1998b; Peretti and Willemart, 2007; Hrušková-Martišová et al., 2008a, 2010a). Whereas in adult females the primary function of the chelicerae remains feeding, the chelicerae of adult males, which are often markedly dimorphic, serve a crucial secondary function—reproduction. The exact role of the chelicerae during mating remains poorly understood, however. The chelicerae are thought to subdue a struggling female (e.g., holding her hind leg), to induce or play a part in inducing a state of temporary paralysis, to prepare the female for mating, and/or to transfer the sperm to the female gonopore (Heymons, 1902; Cloudsley-Thompson, 1961, 1967a, 1967b; Amitai et al., 1962; Junqua, 1962; Muma, 1966b; Wharton, 1987; Punzo, 1998b; Peretti and Willemart, 2007; Hrušková-Martišová et al., 2008a, 2010a).

Among many arthropods, adult males often exist solely for reproduction, and are short-lived and unable to feed. This switch in primary function is usually accompanied, on one hand, by reduction or absence of structures associated with feeding and, on the other, by modification of structures for sperm transfer and other aspects related to mating. This is true for many arachnids. Examples of arachnids in which one pair of prosomatic appendages is modified to function as an intromittent organ include the pedipalps of Araneae and the third pair of legs of Ricinulei. Solifugae are the only arachnid order in which the chelicerae are modified for mating, often as an intromittent organ, and thus the only chelicerate that carries a large percentage of secondary sexual characters on the chelicerae (Kraepelin, 1908a; Hewitt, 1919b; Roewer, 1932–1934). In addition to reduced or modified dentition, other sexually dimorphic cheliceral modifications include size and shape, shape of the **cheliceral fingers** (mainly the dorsal or fixed finger) and especially the apices thereof, **chaetotaxy**, processes and carinae, and the presence of a **male flagellum** or **flagellar complex**.

Although little is known about the functional morphology of solifuge chelicerae, the richness in characters associated with these structures highlights their importance in many aspects of solifuge behavior, especially mating (tables 1–4). Unsurprisingly, cheliceral characters are of fundamental importance for solifuge systematics, from species to family level. The primary charac-

TABLE 4

Female reproductive tract morphology in families of Solifugae for which data available

Based on Dufour (1861: 433), Birula (1892), Bernard (1896), Warren (1939), Vachon (1945), and Klann (2009).

	Pouches on genital chamber[a]	Oviduct	Ovary
Ammotrechidae Roewer, 1934	laterally	diameter approximately uniform along oviduct	oocytes develop outside ovary, lateral side only
Eremobatidae Kraepelin, 1901	absent	strongly narrows before entering genital chamber	″
Galeodidae Sundevall, 1833[b]	small; distally on chamber, between oviduct entry points	diameter relatively uniform along oviduct	″
Rhagodidae Pocock, 1897	glands present, homologous with pouches?	unknown	″
Solpugidae Leach, 1815[c]	absent?	comprises: oviduct proper,[d] oviducal chamber,[e] narrow connecting tube, glandular tube	″

[a] Genital chamber and oviduct surrounded by strong longitudinal and transverse muscles; pouches surrounded by thin muscle layer (Vachon, 1950; Klann, 2009).

[b] Also see Dufour (1861: 433, pl. 4, fig. 26).

[c] Dufour's (1861) pl. 4, fig. 27b does not agree with the figures and discussions of Warren (1939: 143, fig. 2) and Vachon (1945: 478, fig. 1).

[d] Oviduct proper enters oviducal chamber by curving back upon itself and opening into chamber through comparatively small, anteriorly directed tube (see Warren, 1939: 143, fig. 2 d, e).

[e] Oviducal chamber holds seminal fluid (Vachon, 1945) and is lined with thin layer of ectodermal epithelium (Warren, 1939).

ter systems of the chelicerae include the dentition, male flagellar complex and chaetotaxy. The dentition and the male flagellum are covered in detail in the present contribution. Other character systems discussed more briefly include the shape of the cheliceral **manus** and fingers, chaetotaxy, the **stridulatory apparatus** and the integument (flanges, carinae, **granulation** and **cuticular canals**, sensory structures, etc.).

On Homology and Terminology

The concept of homology is fundamental to comparative biology (Bock, 1973; Assis, 2014). Statements of homology provide the foundation for the explanatory and predictive power of phylogenetic hypotheses and the classifications derived from them (Patterson, 1982; De Pinna, 1991; Brower and Schawaroch, 1996; Rutishauser and Moline, 2005; Schuh and Brower, 2009). Patterson (1982, 1988) proposed three tests of homology: similarity (in form and topographical correspondence, i.e., position), conjunction, and congruence. According to Patterson (1988: 605), similarity validates a character as worthy of testing, conjunction reveals what is not homologous, and congruence tests for synapomorphy. De Pinna (1991) clarified the discovery of homology as a two-step process, whereby primary homology refers to statements based on structural and positional similarity, proposed a priori to the construction of a character matrix, and secondary homology, i.e., primary homology that is corroborated by a test of congruence with other characters (during phylogenetic analysis). Primary homology assessment was further subdivided into two steps by Brower and Schawaroch (1996: 266): topographic identity represents the discovery of characters ("comparable features among taxa") which represent the columns in a character matrix, whereas character-state identity yields hypotheses of homology within these characters, the scoring of character states. Patterson's (1982) approach to homology assessment, which Brower and Schawaroch (1996: 266) summarized as "conjectural homology assessment prior to cladistic analysis" (homology as similarity) and "corroborated homology assessments after cladistic analysis" (homology as synapomorphy), has been widely accepted by the systematics community. Primary homology is recognized as an integral part of character analysis prior to phylogenetic analysis (e.g., Delfino et al., 2010; Maidment and Porro, 2010; Vogt et al., 2010; Candela and Rasia, 2012) and, indeed, as "the prime determinant of the outcome of cladistic analysis" (e.g., Hawkins et al., 1997: 278). Hypotheses of primary homology represent potential synapomorphies to be coded into a character matrix and tested for secondary homology. Those that pass the test of congruence with other characters in a phylogenetic analysis become the synapomorphies upon which taxonomic classifications are based.

Even when primary homology determination is not part of tree building, detailed character analysis remains essential (e.g., Ramírez, 2007: 15) and some have argued that character analysis and description should precede primary homology assessment (Vogt et al., 2010: 303). Morphological data are most appropriately used for phylogeny reconstruction when hypotheses of homology are unambiguous (Scotland et al., 2003) but this is not straightforward, as "morphological character analysis requires considerable effort, involving many methodological decisions and implicit assumptions at every step of the process" (Wiens, 2001: 689).

Accurate terminology is integral to the primary homology assessment of morphological characters, providing the vocabulary for defining characters recognized by similarity in structure and position. More generally, the translation of observations into descriptive statements "is crucial for the outcome of all subsequent scientific reasoning and the entire scientific argumentation" because it conceptualizes sensory input (Vogt et al., 2010: 303).

Delimitation and description of morphological characters may precede or accompany their assessment for primary homology. However, whereas statements of homology remain hypotheses subject to change, terminology is fixed. Therefore, the terms (vocabulary) applied to characters should reflect similarity, not necessarily hypotheses of putative homology.

Formulating a terminology is not trivial. The comparative approach, among the most important in biological research, requires data to be comparable and communicable (Edgecombe, 2008; Fusco, 2008; Bonato et al., 2010; Richter et al., 2010; Scholtz, 2010). Identified as "the core problem of morphological data" (Vogt et al., 2010: 309), terminology that is not standardized among authors, studies, and scientific communities, the "linguistic problem of morphology" reduces the communication and comparison of data, resulting in incomplete descriptions and the introduction of errors into character matrices, analyses, and classifications. Addressing this problem is a long and laborious process (Vogt et al., 2010: 308):

> Tracing back the different applications of a specific term by different authors and in different periods of time…is usually time-consuming as one has to translate every single paper into one's own terms and definitions. In some cases, due to lack of a comprehensible documentation and lack of voucher specimens, this translation is impossible. As long as such effort is not recorded and made publicly accessible, it has to be conducted by every morphologist anew, which significantly slows scientific progress.

Such a scenario could not be more true for Solifugae, in which few characters are unambiguously defined, terminology is used inconsistently and without explanation, and region-specific usage (e.g., different terminology used by workers in the United States, Latin America, and Africa) is commonplace. Terms were seldom defined in the historical literature, leaving much open to interpretation (appendix 1). An example of terms applied differently in the historical literature is the use of "flagellum" to refer to the ventral of the two flagellar structures in the karschiid *Eusimonia* Kraepelin, 1899, by, e.g., Hirst (1908: 247), Birula (1913: 321) and Kraepelin (1901: 140) versus the dorsal of the two structures by, e.g., Roewer (1934: 299), or both structures by, e.g., Kraepelin (1908a: 222). Such inconsistent applications of terms not only hinders navigation through historical literature, but may lead to erroneous descriptions and character coding. Contradictory usage of terminology is not restricted to older literature. More recent examples are discussed in the relevant sections.

MATERIALS AND METHODS

Literature Survey

During the course of the study presented here, nearly 700 publications, representing over 50% of the literature on solifuge morphology, systematics, and behavior from Linnaeus to the present, were consulted to collate and synthesize existing terminology and hypotheses of homology. This literature included the seminal papers on the order (e.g., Koch, 1842; Simon, 1879; Dufour, 1861; Bernard, 1896; Kraepelin, 1899, 1901; Sørensen, 1914; Roewer, 1934), as well as major regional works (e.g., Putnam, 1883; Purcell, 1899; Banks, 1900; Birula, 1913, 1938; Hewitt, 1919b; Lawrence, 1955; Muma, 1951, 1970a; Wharton, 1981; Maury, 1984). Although every effort was made to cover existing literature as comprehensively as possible, some important works could not be treated as extensively, notably Birula (1938) on the Solifugae of the former USSR, published in Russian.

Given the importance of the context in which terms were used, page numbers are provided for in-text citations or obscure usages. Published figures and plates, often essential to understand the morphological character interpretations of previous authors, are referenced as thoroughly as possible. If an image belongs to another paper, it follows the citation year after a colon; if the image is part of the present publication, a semicolon separates it from cited papers. Following others (e.g., Lawrence, 1965b; Muma 1976; Shultz, 2007), Roewer's (1932–1934) monograph, published in five parts over three years (issues 1–5), is cited using only the 1934 date, followed by a page number, where applicable, to facilitate reference to the year of print.

Taxon Sampling

Exemplar species (Prendini, 2001) were chosen to represent the breadth of taxonomic and morphological diversity in Solifugae, to the extent possible, given the availability of high quality, intact material. Consequently, some enigmatic genera, such as *Toreus* Purcell, 1903 (Ceromidae Roewer, 1933) and *Syndaesia* Maury, 1980 (Daesiidae Kraepelin, 1899), were omitted, and the Asian Gylippidae Roewer, 1933, as well as some subfamilies and genera within the diverse Daesiidae, less well sampled. Despite the paucity of well-preserved material for many solifuge taxa, the sample included monotypic genera of uncertain placement, such as the daesiids, *Ammotrechelis* Roewer, 1934 and *Ceratobiton* Delle Cave and Simonetta, 1971, the monotypic subfamilies Dinorhaxinae Roewer, 1933 and Namibesiinae Wharton, 1981, and an adequate representation of enigmatic higher-level taxa such as Ceromidae, Hexisopodidae Pocock, 1897, Lipophaginae Wharton, 1981, and Melanoblossiinae Roewer, 1933, each including representatives of several genera. Sampling was slightly skewed toward southern African taxa, which comprise approximately 29% of the world's genera and 16% of the world's species, as well as families Eremobatidae Kraepelin, 1901 and Solpugidae Leach, 1815, which are part of larger studies and were more readily available. In total, 510 specimens, representing all 12 solifuge families and 17 of the 19 subfamilies, 64 genera (46% of the total) and 188 species (17% of the total) were examined (appendix 2), of which 157 species representing 49 genera, and all 17 subfamilies that were examined, were illustrated (figs. 1–26; pls. 1–159); 45 species were represented by both sexes. The generic representation is in all likelihood artificially depressed, given the unnatural generic classification of several families, e.g., Rhagodidae Pocock, 1897, which Lawrence (1956: 120) euphemistically described as "a fantastic proliferation of genera."

Material Examined

Material examined is deposited in the following collections: American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CAS); Denver Museum of Nature and Science, Colorado (DMNS); Hebrew University of Jerusalem, Israel (HUJI); Kirikkale University, Turkey (KUT); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Musée Royal de l'Afrique Central, Tervuren, Belgium (MRAC); National Collection of Arachnida, Plant Protection Research Institute, Pretoria, South Africa (NCA); National Museum of Namibia, Windhoek, Namibia (NMNW); KwaZulu-Natal Museum, Pietermaritzburg, South Africa (NMSA); Senckenberg Museum, Frankfurt, Germany (SMF), including the Roewer collection (R); Tel Aviv University, Zoology Museum, Israel (TAUZM); Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa (TMSA); Zoological Museum, Lund University, Sweden (ZMLU); Zoologisches Museum der Universität Hamburg, Germany (ZMUH).

Species Identification

An attempt was made to identify the material examined to species as accurately as possible but, given the inadequacy of keys and the general absence of modern revisions, misidentifications at the species level cannot be ruled out. Species identification is particularly difficult for females. Females lack a cheliceral flagellum, and their chelicerae and associated characters are conserved and mostly uniform among species, and in some cases among genera and families. Roewer (1934) provided keys to females, but these proved unreliable (Lawrence, 1955: 153) and several authors (e.g., Hewitt, 1919b; Turk, 1960) cautioned against identifying females. Interspecific variation in female opercular shape permits identification of females in three taxa only: Eremobatidae (e.g., Muma, 1951), Gylippinae Roewer, 1933 (e.g., Birula, 1913), and Karschiidae Kraepelin, 1899 (e.g., Gromov, 2003a). Some immatures remain impossible to identify to species, and sometimes even to family, unless collected as part of larger series. With few exceptions, species identification therefore depends on adult males (e.g., Lawrence, 1963), and primarily on the cheliceral characters thereof. In the present study, females were usually identified by reference to series that included adult males. Conclusions were based on large series wherever possible, but for many taxa these were unavailable, or of inadequate quality.

Dissections and Specimen Preparation

Hypotheses of homology were formulated and applied based on comparison of specimens rather than illustrations. Line drawings seldom portray subtle differences in size and sclerotization, whereas photographic images may not accurately represent relative sizes, depending on the angle and extent of illumination. Manipulation of chelicerae is usually required to assess the relative overlap of dentition, which cannot be inferred from illustrations. Illustrations in the literature were, however, of value for estimating character diversity.

When permitted by curators, a chelicera was removed for examination, because manipulating free chelicerae was found to result in less damage to fragile, taxonomically important characters such as **setae**. The dextral chelicera was usually removed, except when damaged, by carefully cutting through the **cheliceropeltidial articular membrane (cpam)**, ligaments, and muscle tissues at its base with a pair of ophthalmic scissors, thereby freeing the **condyle** from its socket in the cheliceropeltidial articulation, taking care not to cut through the chitinous layer or damage the rostrum. Removing cheliceral setae to expose the teeth and detail of the dorsal finger, and to indicate the origins of setae, is common practice among New World workers, and useful especially in Eremobatidae, but should be discouraged when few specimens are available because of the damage to characters of potential importance for solifuge systematics. No setae were removed during the present study but, where found to have been previously removed, setal origins were indicated in figures.

Chelicerae preserved with the fingers closed were opened to expose all teeth. When permitted by the curator, closed fingers were relaxed using a method recommended by Muma (1985). The chelicera was placed in a small, open vial containing approximately 20% ethanol and heated in a microwave oven, or with a hair drier, for ca. 1–2 minutes, depending on the size of the chelicera. This treatment usually loosened the tissue sufficiently to facilitate opening the fingers without risk of damage. The pattern of closure and overlap of the fixed and movable finger dentition was also examined. When cheliceral fingers are open, it is not always apparent how teeth will overlap when the fingers are closed (see pl. 25A–C). To determine this pattern, the fingers of some specimens were forcibly closed using minuten pins inserted into silicon sealant set to harden.

Microscopy and Imaging

Materials were examined using a Nikon SMZ 1500 stereoscope (AMNH) and an Olympus CKX41 compound scope (Colorado State University, Fort Collins). Most cheliceral images were taken with a Nikon D300 camera mounted on a Microptics ML-1000 digital-imaging system at the AMNH. The focal planes of single image stacks were combined with CombineZM software (Hadley, 2012). A typical stack comprised 10–15 images, although the number ranged from three to 40. Most images of Eremobatidae (pls. 65, 67, 68, 70, 72, 76, 79, 82) and a few species belonging to other families were taken with a Canon 5d (Passport II, Visionary Digital system) and combined using Zerene Stacker (Littlefield, 2013) at the DMNS. Some images of Daesiidae (pls. 142, 143, 144) and Solpugidae (pls. 102E–H, 109A–F, H, 124E, F) were taken with a Leica EZ40 digital stereoscope. Line drawings were prepared by tracing digital images on a Wacom (Intuos4) tablet, while simultaneously checking the specimen imaged under a stereoscope for accuracy, especially if dentition was partially obscured by setae in the image. Adobe Photoshop CS6 was used for editing images and drawings. Scanning electron microscopy (SEM) was used to image morphological structures that could not be clearly illustrated with other techniques. Specimens were critical-point dried and sputter coated with gold-palladium (40/60) prior to SEM with a JEOL 5600 at Lund University, Sweden, a Hitachi S4700 FE-SEM at the AMNH, or a JEOL-JSM 6500F at Colorado State University.

Primary Homology Assessment

A major aim of the present contribution was to survey the cheliceral characters and character systems of Solifugae and develop hypotheses of primary homology. Primary homology was assessed using the criteria of Remane (1952) and Patterson (1982, 1988). Remane's (1952) three criteria are position (similarity in topology, including similarity in relation or connectivity), structure (similarity in form), and continuum (linkage of intermediate forms). Patterson's (1982, 1988) three tests of homology include two of relevance to primary homology assessment, i.e., similarity (in form and topographical correspondence) and conjunction (two structures observed on the same individual organism cannot be homologous). Topographical (positional) similarity is often the most powerful criterion (Rutishauser and Moline, 2005). There may be conflict among the criteria, e.g., similarity in position but difference in structure (Ramírez, 2007). Such conflict was encountered in the male cheliceral dentition and flagellar character systems, due to a diversity of structures and differences in cheliceral shape. These conflicts were resolved by applying additional, character-specific criteria to discriminate among alternative hypotheses of similarity in form (in dentition; table 7) or position (male flagellum). Where competing hypotheses remained, the most plausible were advanced, with alternatives mentioned to permit testing in future analyses (e.g., indicator hypotheses concept; Rieppel, 2005: 25; Ramírez, 2007).

The positional homology of flagella was determined by reference to landmark teeth, rather than by comparing the absolute positions of flagella on the chelicera. The position of the point of attachment of the flagellum, relative to a particular tooth, was determined by drawing a line parallel to the **gnathal edge** of the fixed finger and a second line, perpendicular to the first and passing through the point of attachment (see pl. 44).

Terminology and Conventions

Another aim of the present contribution was to develop an accurate, concise, and unambiguous (Gordh and Headrick, 2001) terminology for characters hypothesized to be homologous based on similar structure and position. In developing terminology, current and traditional usages were considered to facilitate stability, and many of the terms applied here are not new to the solifuge literature, e.g., *fond* (Putnam, 1883; Fichter, 1940; 1941; Muma, 1970b) and *distal tooth* (Millot and Vachon, 1949). Some guidance was obtained from terminology applied to other arachnid taxa, e.g., *paturon*, from the spider literature (Ramírez, 2014). However, information content (especially descriptive accuracy), comparability among characters within a character system (e.g., among different series of setae on the prolateral surface of the chelicera), and consistency were given primacy over legacy usage. Standardized abbreviations were developed to render some positional terminology more concise.

As the aim was for accurate and intuitive terminology, reasons for the choice of terms are not elaborated, except in the case of *pro-* and *retrolateral* as descriptors for the opposing lateral surfaces of the chelicerae. These terms for cheliceral orientation, which have not previously been used to describe solifuge morphology, form the basis of many other terms newly proposed here.

There is no consensus in the solifuge literature regarding the terminology for cheliceral orientation, despite its importance for understanding position. The terms *inner* and *outer*, and variants thereof, viz. *internal*, *external*, *interior*, *exterior*, and *adaxial*, are common (e.g., Dufour, 1861; Purcell, 1899; Hewitt, 1919b; Lawrence, 1931, 1955; Mello-Leitão, 1938; Panouse, 1960a, 1960b; Levy and Shulov, 1964; Simonetta and Delle Cave, 1968; Wharton, 1981; Maury, 1984; Armas, 1994; Klann and Alberti, 2010). Other authors used *medial* or *median* and *lateral* (Roewer, 1934; Kraus, 1956; Turk, 1960; Wharton, 1981; Reddick et al., 2010). Hewitt (1919b: 24) used *mesial* (also used by Brookhart, 1965) interchangeably with *inner*. Muma (1951) introduced *mesal* (inner) and *ectal* (outer), terminology subsequently followed by most workers in the New World, especially in the United States (e.g., Brookhart and Cushing, 2004, 2008; Catenazzi et al., 2009; Carvalho et al., 2010), and by some in the Old World (e.g., Gromov, 1993).

Unfortunately, none of the aforementioned terms are accurate descriptors of orientation as per their definitions. *Mesal* is defined as "descriptive of structure that is positioned on or in the median plane of the body" (Gordh and Headrick, 2001: 569) and is therefore appropriate for describing the position of the rostrum, but not the surface of the chelicera adjacent to the midline. *Mesial* is defined as "descriptive of something near an imaginary line dividing the body into left and right halves; the median plane of the body" (Gordh and Headrick, 2001: 570). Although more accurate than *mesal* in referring to the surface of the chelicera adjacent to the midline, *mesial* cannot be applied to the pedipalps and legs (appendages serially homologous to the chelicera) and offers no antonym for the opposite surface of the chelicera. *Ectal*, defined as "directed outward or toward the outer surface of the...body" (Gordh and Headrick, 2001: 303), has mistakenly been used as the antonym of *mesial*. However, this term and its antonym, *ental*, along with their respective synonyms, *outer*, *external*, *exterior*, and *inner*, *internal*, and *interior*, more appropriately describe the positions of structures inside versus outside the integument, rather than on the opposing surfaces of the chelicera (see Acosta et al., 2008). *Lateral* is defined as "descriptive of structure or movement relating to the side" (Gordh and Headrick, 2001: 512). As such, its use in referring to the surface of the chelicera adjacent to the midline or to its opposite surface is correct in the same way that "lateral" refers to the side of the body. However, the term fails to distinguish between the two surfaces of the chelicera or to account for the fact that chelicerae are serial homologs of the pedipalps and legs, to which consistent terminology should preferably be applied.

A consensus in terminology among different orders of arachnids is obviously desirable. *Inner* and *outer* are the predominant descriptors of cheliceral orientation, e.g., in Amblypygi (Shear, 1970) and Araneae (Schütt, 2000), although other terms include *mesial* in Scorpiones (Alexander, 1958) and *anterior* and *posterior* (e.g., Platnick, 2000), *prolateral* (Bosselaers and Jocqué, 2002), *frontal* (Bosselaers and Jocqué, 2002), and *pro-* and *retromarginal* (as terminology for specific margins; Gillespie, 1994; Bosselaers and Jocqué, 2002; Ramírez, 2014) in Araneae. Terms of orientation that attempt to reflect the homology of the cheliceral surfaces are complicated by the fact that the chelicerae have undergone considerable rotation, at least in some segments, among the different orders. For instance, the chelicerae of scorpions are set at such an angle that the surface adjacent to the midline in effect faces mesoventrally. The orientation is similar in Opiliones, such that the surface adjacent to the midline and its opposite surface are more commonly referred to as *ventral* and *lateral* (Snegovaya, 1999), respectively. The orthognathous and labidognathous orientations of the chelicerae of spiders (Kraus and Kraus, 1993; Zonstein, 2004) lead to a complicated terminology including *anterior* and *posterior*, *mesal* and *ectal*, and the prefixes *pro-* and *retro-* to refer to different positions on the chelicera (e.g., Ramírez, 2014).

Pro- and retrolateral are commonly used in spider (e.g., Platnick, 2000; Ramírez, 2014) and more recent scorpion literature (e.g., Acosta et al., 2008; González-Santillán and Prendini, 2013) pertaining to the pedipalps and legs, the lateral surfaces of which face forward (pro-) or backward (retro-). The chelicerae, pedipalps, and walking legs are accepted as serial homologs in chelicerates (Boxshall, 2013). Therefore, the terms *pro-* and *retrolateral* are appropriate to describe the homologous surfaces of all these appendages, despite the fact that the chelicerae do not project laterally like the pedipalps and legs.

The terms *prolateral* and *retrolateral*, considered more accurate in accounting for position and serial homology, are applied throughout the present contribution to describe the surfaces of the chelicera respectively facing toward and away from the midline of the body. Subdivision and fusion of these terms with others referring to topological position creates precise positional descriptors for structures situated on different surfaces, for example *prodorsal*, *proventral*, *retrodorsal*, *retroventral*, etc.

A glossary of terms (appendix 1), each with a descriptive statement and a list of historical synonyms and interpretations, is provided for reference. Terms in the glossary are indicated in boldface on first mention in the text. The glossary provides more than a dictionary of terms, however; it supplements character discussions in the text, as each term in the glossary is referred to in the annotated illustrations of voucher specimens. Interpreted illustrations accompanying character descriptions provide empirical substantiation for descriptive statements and increase the transparency of data (Vogt et al., 2010).

Other terms and phrases used throughout include "distally directed," "proximally directed," and "sclerotization." "Distally directed" and "proximally directed" refer to position with respect to the chelicera, i.e., directed anteriorly or posteriorly with respect to the body, respectively. “Sclerotization” refers to the darkness of the cuticle, assumed to be a function of the density thereof, and not to the density of pigmentation (or infuscation).

A comparative approach is followed throughout. All discussions and examples pertain to male characters, unless stated otherwise. In order to assist with orientation, illustrations were standardized such that the distal side of the chelicera faces left in prolateral view and right in retrolateral view, with few exceptions.

Discussions of functional morphology require understanding current knowledge of reproductive behavior. Muma (1966b) identified three phases in mating behavior (attack, contact, and release) but overlap in behaviors and assumptions of function fail to accommodate observations of mating in non-eremobatid taxa. Male reproductive behavior is here divided into three main phases (somatic contact phase, genital contact phase, and release phase), each with further subdivisions (table 2).

Abbreviations

Abbreviations referring to dentition or related terms are in capitals, those referring to setation in lowercase italics, and all other terms in lowercase.

BF	basifondal teeth
cgn	coxal gland nozzle
cgns	coxal gland nozzle setae
cgs	coxal gland setae
cpam	cheliceropeltidial articular membrane
cpc	cheliceropeltidial condyle
dfs	dorsal flagellar seta
ecpca	external cheliceropeltidial condylar attachment
fcp	flagellar complex plumose seta/e
fcs	flagellar complex subspiniform to spiniform setae
FD	fixed finger, distal tooth
fg	flagellar groove
FGP	flagellar groove process
fiam	fondal interdigital articular membrane
FM	fixed finger, medial tooth
FN	fondal notch
FP	fixed finger, proximal tooth
FSD	fixed finger, subdistal tooth/teeth
FSM	fixed finger, submedial tooth/teeth
FST	fixed finger, subterminal tooth/teeth
FT	fixed finger, terminal tooth
iam	interdigital articular membranes
lo	lyriform organ
mff	movable finger, fondal setae
MM	movable finger, medial tooth
MN	medial notch
mo	mucron organ
MP	movable finger, proximal tooth
mpd	movable finger, prodorsal setae
MPL	movable finger, prolateral tooth
MPLC	movable finger, prolateral carina
mpm	movable finger, promedial setae
mpv	movable finger, proventral setae
MRLC	movable finger retrolateral carina
MSM	movable finger, submedial tooth/teeth
MSP	movable finger, subproximal tooth/teeth
MST	movable finger, subterminal teeth
MT	movable finger, terminal tooth
MVE	medioventral excrescence
mvo	medioventral organ
pdd	prodorsal distal setae
pddm	prodorsal distal margin
pdp	prodorsal proximal setae
pdsc	prodorsal spiniform setal cluster
PF	profondal teeth
PFM	profondal medial tooth
PFP	profondal proximal tooth
PFSM	profondal submedial tooth
PFSP	profondal subproximal tooth
pic	prolateral interdigital condyle
PLDP	prolateral dental process
pm	promedial setae
pmpc	promedial proximal setal cluster
principal rlf	principal retrolateral finger setae
pv	proventral setae
pvd	proventral distal setae
pvdm	proventral distal margin
pvsd	proventral subdistal setae

pvsd (comb)	proventral subdistal setal comb
RDP	retrodorsal process
RF	retrofondal teeth
RFA	retrofondal apical tooth/teeth
RFM	retrofondal medial tooth
RFP	retrofondal proximal tooth
RFSM	retrofondal submedial tooth/teeth
RFSP	retrofondal subproximal tooth/teeth
ric	retrolateral interdigital condyle
rlf	retrolateral finger setae
rlm	retrolateral manus setae
rlms	retrolateral manus spiniform seta
rlpc	retrolateral proximal setal cluster
sfc	setiform flagellar complex
sme	socket margin elevation
STF	subterminal flange
vdp	ventral digital plagula
vfs	ventral flagellar seta
viam	ventral interdigital articular membrane
vmp	ventral manus plagula
VN	ventral notch on movable finger

TAXONOMIC OVERVIEW

Solifugae Sundevall, 1833

Currently, 12 extant families comprising 139 genera (Harvey, 2003; Prendini, 2011) and 1105 species are recognized within Solifugae. Thirty-four species have been added to the 1075 species listed by Harvey (2003), six species of Ammotrechidae Roewer, 1934, one species of Daesiidae, 17 species of Eremobatidae, one species of Gylippinae, five species of Karschiidae, and four species of Mummuciidae Roewer, 1934, while five species of Eremobatidae were synonymized (Brookhart and Cushing, 2002; 2004; 2005; 2008; Gromov, 2003a; Martins et al., 2004; Armas and Teruel, 2005; Rocha and Carvalho, 2006; Ballesteros and Francke, 2007; Catenazzi et al., 2009; Carvalho et al., 2010; Reddick et al., 2010; González Reyes and Corronca, 2013; Karataş and Uçak, 2013; Iuri et al., 2014; Erdek, 2015). The most speciose families are Galeodidae Sundevall, 1833 (199 species), Solpugidae (191 species), Daesiidae (190 species), and Eremobatidae (187 species). Understanding the current family, subfamily, and generic level taxonomy of the group is necessary for evaluating patterns of character variation. A list of taxa and material examined follows in appendix 2.

Ammotrechidae Roewer, 1934

Ammotrechidae (fig. 1M; pls. 146–148, 149A–D, 150, 153G, H) are restricted to the New World, the southern half of the United States (northern California to Florida), Mexico, the Caribbean, and South America, with greatest diversity in the arid to semi-arid northern and western parts of South America. The family is divided into five subfamilies, Ammotrechinae Roewer, 1934, Mortolinae Mello-Leitão, 1938, Nothopuginae Maury, 1976, Oltacolinae Roewer, 1934, and Saronominae Roewer, 1934, and includes some genera of uncertain placement (Harvey, 2003). Harvey's (2003) list of 22 extant genera did not reflect the transfers of *Mummuciona* Roewer, 1934, and *Sedna* Muma, 1971, from Mummuciidae to Ammotrechidae (Maury, 1976, 1982, 1987) which, together with the subsequent synonymy of *Ammotrechella* Roewer, 1934, with *Ammotrechona* Roewer, 1934, by Armas (2004), brings the number of extant ammotrechid genera to 23. The fossil species *Happlodontus proterus* Poinar and Santiago-Blay, 1989, a putative immature described from Dominican amber, is also placed in Ammotrechidae. Ammotrechidae are defined primarily on the immovable, membranous, elliptical, and bowl-shaped flagellum. According to Muma (1971), the flagellum is the only character by means of which Daesiidae and Ammotrechidae (and Mummuciidae) can be differentiated, rendering identifications of singleton females almost impossible, even to family. Since Harvey's (2003) catalog, six ammotrechid species have been described, four by Armas and Teruel (2005), one by Catenazzi et al. (2009), and one by Iuri et al. (2014), raising the number of species in the family to 89. Four subfamilies, six genera, and six species were examined during the present study.

Ceromidae Roewer, 1933

Ceromidae (pls. 91–96) is a small family, currently containing three extant genera and 20 species, recorded from southern and eastern Africa, and the fossil *Cratosolpuga wunderlichi* Selden, 1996, from the Crato Formation in Brazil. *Ceroma* Karsch, 1885 and *Ceromella* Roewer, 1933 exhibit clear affinities including similar dentition and a distinct flagellar complex comprising an elongated, paraxially rotatable flagellum with a capsular base situated behind a row of stiff modified setae, the **flagellar complex plumose (*fcp*) setae**. *Toreus* is a monotypic genus of unclear affinities (Muma, 1976; Wharton, 1981), known from a single specimen. A flagellum is absent in the type species, *Toreus capensis* (Purcell, 1899), but the dorsal cheliceral fingers are highly modified. Lawrence (1962b) suggested that the holotype is a female, the male being the paratype of *Solpuga grindleyi* Brown, 1961 (currently in synonymy with *Blossia litoralis* Purcell, 1903), a species originally placed in Solpugidae notwithstanding that the flagellum and associated setae are consistent with the flagellar complex of Ceromidae as described above. Lawrence (1962b) did not formally synonymize these taxa, however, and it is unlikely, based on the extreme modification of the cheliceral fingers, that the holotype of *Toreus*, which was not examined during the present study, is female. If the holotype is indeed male, the absence of a flagellum suggests an affinity with Lipophaginae (vide Wharton, 1981), but Muma (1976) retained *Toreus* in Ceromidae presumably based on characters shared with ceromids, notably two claws on the tarsi of leg I. *Toreus capensis* may prove to be an intermediate form between Ceromidae and Lipophaginae. According to Hewitt (1919b: 63), the fixed (dorsal) finger is "divided into two portions." This seems to resemble the **dorsal hornlike process** that is fused to the **fixed (dorsal) finger** in *Trichotoma michaelseni* (Kraepelin, 1914) (pl. 88C). Additional specimens of *Toreus* are required to resolve its phylogenetic position. Two genera and four species of Ceromidae were examined during the present study.

Daesiidae Kraepelin, 1899

Daesiidae (fig. 1I, J; pls. 132–145, 153A–F) is a large, diverse family, with a broad distribution including Africa, southern Europe, the Middle East, central Asia, and South America (Argentina and Chile), and is the only family occurring in the New World and the Old World. Daesiidae are probably paraphyletic, however.

Kraepelin (1899) established subfamily Daesiinae Kraepelin, 1899 within Solpugidae, based partly on the husk-, bladder-, or vase-shaped flagellum. Roewer (1934: 344, 346) elevated Daesiinae to family rank, again mostly on the basis of the rotation, shape, and membranous character of the flagellum and relied heavily on tarsal segmentation (tarsi of legs II and III with one or two true segments, or tarsomeres, and of leg IV with one to four tarsomeres), the absence of claws on leg I, and the form of the flagellum for the classification of the family. Daesiidae are currently divided into six subfamilies, Daesiinae, Gluviinae Roewer, 1933, Gluviopsinae Roewer, 1933, Gnosippinae Roewer, 1933, Namibesiinae, and Triditarsinae Roewer, 1933; however, these subfamilies do not accommodate all taxa, and have been largely ignored in the taxonomic literature (for details, see Wharton, 1981). Wharton (1981) described Namibesiinae to accommodate the Old World genus *Namibesia* Lawrence, 1962 (pls. 132A–D, 133). The monotypic *Syndaesia*, restricted to the New World, resembles *Namibesia* but Maury (1985) suggested that these similarities are superficial and the two genera are not closely related. Generic definitions within Daesiidae remain untested, and various workers have called for reevaluation of generic characters (Delle Cave and Simonetta, 1971; Wharton, 1981; Muma, 1982; Reddick et al., 2010). For example, two distinct species groups are recognized within *Hemiblossia* Kraepelin, 1899, the *bouveri* group (pls. 139G, H, 141A, B, 142) and the *australis* group (pls. 139I, J, 141C) (Wharton, 1981). Wharton (1981) suggested these groups may be united by convergent characteristics based on shared termitophilous habits.

Family Amacataidae Muma, 1971, was created to accommodate *Amacata penai* Muma, 1971, a New World species later synonymized with *Ammotrechelis goetschi* Roewer, 1934, by Maury (1985) (pls. 132E–H, 134). Muma (1971: 17) separated Amacataidae from Ammotrechidae on the basis of the complex, rotatable cheliceral flagellum and from Daesiidae on the basis of the "distinctive flagellum...[and] unusual tarsal segmentation and spinelike setal armature of the tarsi." Arguing that the flagellum is not that different and that the tarsal segmentation and "spination" of legs II–IV falls within the range of variation observed within Daesiidae, Maury (1980a) synonymized Amacataidae with the latter. The Baltic amber fossil *Palaeoblossia groehni* Dunlop et al., 2004 is placed within Daesiidae. Only one extant species of Daesiidae has been described (Reddick et al., 2010) since Harvey's (2003) catalog, raising the number of species in the family to 190. Five of the six subfamilies, 10 genera, and 30 species were examined during the present study.

EREMOBATIDAE KRAEPELIN, 1901

Eremobatidae (fig. 1L; pls. 65–84), restricted to North America, i.e., southeastern Canada, the United States west of the Missouri-Mississippi rivers (Maury, 1984), and Mexico, is the most speciose family of Solifugae in the New World (Harvey, 2003). Muma (1951, 1989) recognized two subfamilies, based mainly on the number of claws on tarsus of leg I: Eremobatinae Kraepelin, 1901, comprising *Eremobates*, *Eremocosta* Roewer, 1934, *Eremorhax* Roewer, 1934, *Eremothera* Muma, 1951, *Horribates* Muma, 1962; and Therobatinae Muma, 1951, comprising *Chanbria* Muma, 1951, *Eremochelis* Roewer, 1934, *Therobates* Muma, 1951 (currently a junior synonym of *Eremochelis*, synonymized by Muma, 1970a), and *Hemerotrecha* Banks, 1903. Muma (1989) provided a historical synopsis of the taxonomy of Eremobatidae post-Roewer (1934). This was supplemented by the annotated checklist of Brookhart and Brookhart (2006). Seventeen species have been described and five synonymized since Harvey's (2003) catalog (Brookhart and Cushing, 2002, 2004, 2005, 2008; Ballesteros and Francke, 2007), resulting in 187 species currently described. Males are recognized by a narrow, often **styletlike** fixed (dorsal) finger and a cluster of modified setae, which forms a **type A setiform flagellar complex (*type A sfc*)**. The presence of a dorsal terminal spiniform macroseta on tarsi II and III (Muma, 1976) may be a synapomorphy for the family. Both eremobatid subfamilies, 8 genera and 40 species were examined for the present study.

GALEODIDAE SUNDEVALL, 1833

Galeodidae (fig. 1A, B; pls. 59–63, 64K, L) is currently the most speciose family of Solifugae, with a largely Palearctic distribution in north Africa, the Middle East, and central Asia, extending to the Indian subcontinent. No subfamilial divisions are recognized. The family presently includes nine genera and 199 species, 173 of which are placed in *Galeodes* Olivier, 1791. Five galeodid genera, *Galeodumus* Roewer, 1960, *Gluviema* Caporiacco, 1937, *Paragaleodiscus* Birula, 1941, *Roeweriscus* Birula, 1937, and *Zombis* Simon, 1882, are monotypic. *Gluviema migiurtina* Caporiacco, 1937, described on the basis of a single female, was erroneously placed in Daesiidae, and Delle Cave and Simonetta (1971) speculated it should be transferred to *Galeodellus* Roewer, 1934, formerly a subgenus of *Galeodes*. The validity of *Paragaleodiscus aflagellatus* Birula, 1941, described on the basis of seven males, 18 females, and 10 juveniles, requires further investigation; it is apparently the only galeodid lacking a flagellum in the adult male. Turk (1960) did not recognize *Roeweriscus* as the diagnostic characters are not unique. *Zombis* is probably a senior synonym of *Paragaleodes* Kraepelin, 1899 (Harvey, 2002a). *Paragaleodes* contains 12 diurnal species, and is the second most speciose galeodid genus after *Galeodes*. The remaining genera, *Galeodopsis* Birula, 1903 and *Othoes* Hirst, 1911, comprise five and four species, respectively. Galeodidae are probably monophyletic. Potential synapomorphies include the presence of setae on the basal claw segment, a comblike structure protecting the abdominal spiracles, and a spoon-shaped, "paraxially and slightly diaxially" (Muma, 1976: 4), hereafter referred to as subdiaxial, rotatable flagellum. However, few morphological characters have been identified on which to base a natural generic division within the family (Turk, 1960) and species delimitation is hampered by the relative uniformity of the male flagellum. Two genera and nine species were examined for the present study.

Gylippidae Roewer, 1933

As currently defined, Gylippidae comprise two diverse groups of taxa with a disjunct distribution. Wharton (1981) placed the Asian genera, *Acanthogylippus* Birula, 1913 and *Gylippus* Simon, 1879, in subfamily Gylippinae, and the southern African genera, *Lipophaga* Purcell, 1903, *Trichotoma* Lawrence, 1968, and the monotypic *Bdellophaga* Wharton, 1981, in Lipophaginae. The subfamilial classification of Wharton (1981) was accidentally omitted by Harvey (2003) but is reflected in Harvey (2013). Gylippinae and Lipophaginae share prominent features such as the number of leg tarsomeres, the claw on leg I, and the separation of the **anterolateral propeltidial lobe** from the propeltidium (Wharton, 1981) as well as more subtle features such as similar **stridulatory setae** and the number and position of eyespots (T.L.B., unpublished data). However, they differ considerably, especially in the nature of the flagellar complex and the presence of prominent spiniform setae in Gylippinae. Due to the morphological disparity between Gylippinae and Lipophaginae, they are treated separately in the presented contribution.

Gylippinae Roewer, 1933

Gylippinae (fig. 1K; pls. 85A–F, 86, 90A, B) comprises only 20 described species, restricted to the Middle East and central Asia. Birula (1913) divided *Gylippus* into four subgenera, *Gylippus*, *Acanthogylippus*, *Anoplogylippus* Birula, 1913, and *Hemigylippus* Birula, 1913, based mainly on the **dental papillae** and the presence and number of dorsomedial spiniform setae, i.e., the **flagellar complex spiniform (*fcs*) seta/e** and the robust **retrolateral manus spiniform (*rlms*) seta**. These taxa alternated between genera and subgenera. Roewer (1934: 310) elevated Birula's (1913) subgenera to genera and added a fifth genus, *Paragylippus* Roewer, 1933. Birula (1938) again treated these taxa, including *Paragylippus*, as subgenera whereas Roewer (1960) treated the taxa occurring in Afghanistan, i.e., *Anoplogylippus*, *Gylippus*, and *Paragylippus*, as genera. Gromov and Kopdykbaev (1994) treated the taxa occurring in Kazakhstan, i.e., *Anoplogylippus* and *Hemigylippus*, as subgenera. As a consequence, two genera are currently recognized, *Acanthogylippus* and *Gylippus*, the latter comprising four subgenera, i.e., *Gylippus* (*Gylippus*), *G.* (*Anoplogylippus*), *G.* (*Hemigylippus*), and *G.* (*Paragylippus*). One species of *Gylippus* has been described (Erdek, 2015) since Harvey's (2003) catalog. Two species in different subgenera of *Gylippus* were examined for the present study.

Lipophaginae Wharton, 1981

Lipophaginae (pls. 85G, H, 87–89, 90C–F) comprises seven described species, restricted to southern Africa. No male flagellum, defined as a single modified **dorsal flagellar seta (*dfs*)**, or modified **ventral flagellar seta (*vfs*)**, is present, but a cluster of similarly modified setae, including the ventral flagellar seta (*vfs*) on the fixed finger, forms a **type B setiform flagellar complex (*type B sfc*)**. The extent to which these setae are differentiated from the surrounding setae varies from undifferentiated, e.g., *type B sfc* absent in *Trichotoma michaelseni*, to markedly differentiated, e.g., in *Bdellophaga angu-*

lata Wharton, 1981. All three genera, viz. *Bdellophaga*, *Lipophaga* and *Trichotoma*, and four species were examined for the present study.

Hexisopodidae Pocock, 1897

Hexisopodidae (fig. 1E, F; pls. 126–131) is a small, psammophilous family endemic to southern Africa, comprising 23 described species (Harvey, 2003). The small number of species is probably a sampling artifact due to their cryptic, fossorial habits. The family is defined by a number of unique characters probably related to burrowing, the most obvious being a robust body and short legs (Wharton, 1981). The two genera currently recognized, *Chelypus* Purcell, 1902 and *Hexisopus* Karsch, 1879, are separated by various characters, including the presence of spiniform setae on the pedipalp (Lamoral, 1973) and cheliceral characters described below. Both genera and 11 species were examined for the study.

Karschiidae Kraepelin, 1899

Karschiidae (pls. 50–55, 64A–H) is a small family comprising four genera with a Palearctic distribution in north Africa, the Middle East, and central Asia. Karschiids are partly defined by **multidentate** chelicerae and plumose setae covering the opisthosomal stigmata (Roewer, 1934: 289). *Barrus* Simon, 1880, *Barrussus* Roewer, 1928, and *Eusimonia*, are similar in dentition and flagellar morphology, and distinctly different from *Karschia* Walter, 1889 (pls. 1, 2). *Karschia* is divided into two subgenera, *Karschia* and *Rhinokarschia* Birula, 1935. Four species of *Karschia* (Gromov, 2003a) and one species of *Barrussus* (Karataş and Uçak, 2013) have been described since Harvey's (2003) catalog, raising the number of species in the family to 45. Karschiids are partly defined by **multidentate** cheliderae and plumose setae covering the opisthomal stigmata (Roewer, 1934: 289). Three genera and seven species were examined for the present study.

Melanoblossiidae Roewer, 1933

Melanoblossiidae is a small family restricted to southern Africa, with the exception of the monotypic *Dinorhax* Simon, 1879. Roewer (1934: 339) divided Melanoblossiidae into two subfamilies based on the number of tarsomeres on leg IV: Dinorhaxinae, with two segments, and comprising *Dinorhax* and *Lawrencega* Roewer, 1933, and Melanoblossiinae, with one segment, comprising only *Melanoblossia* Purcell, 1903. Lawrence (1967) criticized use of the number of tarsomeres for separating subfamilies, and transferred all southern African species, including three genera described after Roewer (1934), viz. *Daesiella* Hewitt, 1934, *Unguiblossia* Roewer, 1941, and *Microblossia* Roewer, 1941) to Melanoblossiinae, a classification adopted by Wharton (1981). The inclusion of *Dinorhax* in Melanoblossiidae probably renders this family polyphyletic.

Dinorhaxinae Roewer, 1933

The monotypic subfamily Dinorhaxinae (pls. 56A, B, 57A, B) contains the enigmatic *Dinorhax rostrumpsittaci* (Simon, 1877), the only solifuge species occurring in Southeast Asia (Indonesia and Vietnam). This species was initially placed within Rhagodidae, in the genus *Rhax* Hermann, 1804, which was suppressed in favor of *Rhagodes* Pocock, 1897 (ICZN, 2005), by Roewer (1934: 340), a position that is unlikely to be upheld by phylogenetic analysis. The monotypic genus, *Dinorhax*, was examined for the present study.

Melanoblossiinae Roewer, 1933

Melanoblossiinae (pls. 154–159) currently contains 16 species restricted to southern Africa. All species appear to be diurnal. Melanoblossiids tend to be small in body size, and include the smallest solifuge described to date, i.e., *Lawrencega minuta* Wharton, 1981, with adult males measuring 5–8 mm. Adult males are unknown in *Daesiella* Hewitt, 1934. *Microblossia* Roewer, 1941 is characterized in part by an unmodified flagellar setal complex (Roewer, 1941) comprising three plumose setae at the apex, resembling the flagellar setal complex of Lipophaginae. *Unguiblossia* Roewer, 1941, comprising two species, is diagnosed by the elongate second claw segment, but is in other respects similar to *Lawrencega* (vide Wharton, 1981). *Lawrencega*, *Melanoblossia* and *Unguiblossia* are characterized by a **type C setiform flagellar complex (*type C sfc*)** which consists of modified setae arranged in a well-defined unit prolaterally on the fixed (dorsal) finger. Three species of *Lawrencega*, and three species of *Melanoblossia*, the most speciose melanoblossiid genera, known from both sexes, were examined in the present study.

Mummuciidae Roewer, 1934

Mummuciidae (fig. 1N; pls. 149E–H, 150–152, 153I, J) is restricted to South America and comprises 20 species. The family was initially created as a subfamily of Ammotrechidae (Roewer, 1934: 582) but later elevated to family rank (Maury, 1984: 74) on the basis of the following characters: a vesicle-shaped flagellum with an anterior opening (*una vesicula ovoide*, *con una pequeña abertura anterior*), the absence of pairs of spiniform setae on the pedipalps; and the absence of a **movable finger prolateral (MPL) tooth** (*diente basal interno*). Four mummuciid species have been described since Harvey's (2003) catalog. Three were placed in *Mummucia* Simon 1879 (Martins et al., 2004; Rocha and Carvalho, 2006; Carvalho et al., 2010) whereas one was placed in *Mummucina* Roewer 1934 (González Reyes and Corronca, 2013), the type species of which was recently redescribed (Botero-Trujillo, 2014). The transfer of *Mummuciona* by Maury (1976, 1982) and *Sedna* by Maury (1987) to Ammotrechidae reduced the ten genera of Mummuciidae reported by Harvey (2003) to eight. *Cordobulgida* Mello-Leitão, 1938, *Gaucha* Mello-Leitão, 1924, *Gauchella* Mello-Leitão, 1937, *Metacleobis* Roewer, 1934, *Mummucipes* Roewer, 1934, and *Uspallata* Mello-Leitão, 1938, are monotypic. Most species in the family are placed in the two remaining genera, *Mummucia* (comprising eight species) and *Mummucina* (comprising six species), but mummuciid genera are poorly defined (Maury, 1998; Botero-Trujillo, 2014) prompting recent authors to place new species within the type genus, *Mummucia*, pending a generic revision of the family. Two genera and species were examined during the present study.

Rhagodidae Pocock, 1897

The family Rhagodidae (fig. 1C, D; pls. 56C–H, 57C, D, 58, 64I, J), broadly distributed across north Africa, the Middle East, Asia, and the Indian subcontinent, and characterized by a cylindrical opisthosoma, short, robust legs, robust chelicerae, and a distinct compound structure of two flagella (**diploflagellum**), was recognized as a distinct group early on (Pocock, 1897). Although Rhagodidae will undoubtedly prove to be monophyletic, Roewer's (1934: 264–288) classification is largely uninformative (Lawrence, 1956; Levy and Shulov, 1964). Ninety-eight species are currently recognized. Thirteen of the 27 current rhagodid genera are monotypic, many based on females and juveniles (Roewer, 1934; Harvey, 2003). Conspecifics may key to different genera, depending on whether sinistral or dextral appendages are examined (Lawrence, 1956: 120), potentially preventing reliable identification of genera (e.g., Levy and Shulov, 1964). Cheliceral structure and dentition are very similar among rhagodid species, often even between the sexes (pls. 3C–H; 50–51), and little interspecific variation is evident in the male flagellum, providing few characters for species diagnosis. As with Galeodidae, the other morphologically uniform family of Solifugae, rhagodid taxonomy relies heavily on color patterns (Roewer, 1934) which, according to Turk (1960: 107), appear to be "remarkably constant for most of the Galeodidae and Rhagodidae." Two genera and three species were examined during the present study.

Solpugidae Leach, 1815

Solpugidae (fig. 1G, H; pls. 90G–L, 97–125) is a diverse family, comprising 191 species distributed throughout Africa and the Middle East, easily identified by the six to seven tarsomeres of leg IV (all other families possess one to four tarsomeres) and a unique flagellar morphology comprising a **bulbous base** immovably fixed to the fixed (dorsal) finger, and a chitinous, usually whiplike shaft. Solpugidae are divided into two subfamilies, Ferrandiinae Roewer, 1933, containing a single genus, *Ferrandia* Roewer, 1933, and Solpuginae Leach, 1815, containing the other 16 genera, based on the number of leg IV tarsomeres (six and seven, respectively). Some of the characters presented by Roewer (1934: 420–421), e.g., shape of the deuterosternum and presence of scopula and spiniform setae on the pedipalpal metatarsus, appear to identify broad groups that may prove to be natural (Turk, 1960; Wharton, 1981). However, overt reliance on variable characters, particularly spiniform setae on the legs, resulted in most of the 17 currently recognized genera (Harvey, 2003) being poorly defined. This is especially true for the large genus *Zeria* Simon, 1879, comprising 59 species. Other genera appear to be better defined, e.g., *Zeriassa* Pocock, 1897, the fourth largest genus of Solpugidae, comprising 17 species. *Zeriassa* is one of the most distinct genera in the family, supported by a suite of characters including the shape of the deuterosternum, the propeltidium, the epistomo-labral plate of the rostrum, etc., characters shared with the monotypic *Solpugisticella* Turk, 1960. Several authors (Lawrence, 1955; Turk, 1960; Simonetta and Delle Cave, 1968) identified Solpugidae as one of the families in most urgent need of revision. A synopsis of Solpugidae taxonomy was provided by Wharton (1981). Both subfamilies, 17 genera, and 44 species were examined during the present study.

CHELICERAE

Cheliceral Terminology

The first cheliceral segment, referred to here as the **paturon** in accordance with spider literature (e.g., Ramírez, 2014), comprises the **manus** (i.e., the broad proximal section) and an outgrowth, the **fixed (dorsal) finger** (pl. 1). The manus contains the cheliceral muscles, which extend somewhat into the fixed finger along with the trachea (Klann, 2009; Van der Meijden et al., 2012). Sørensen (1914: 161) mentioned adipose tissue inside the fingers in engorged specimens, but this remains to be verified. The **movable (ventral) finger** is the second cheliceral segment. Although various terminologies have been applied to the cheliceral fingers in the solifuge literature, the term *finger*, or **cheliceral finger**, is preferred here (table 5). Each finger bears dentition (teeth) along its **gnathal edge** (pl. 22), i.e., a **median series** and a **fondal series** of teeth are present on the fixed and movable fingers. The **gnathal edge carina** converges with the **retrolateral edge carina** (distal extension of the **retrolateral longitudinal carina**) and the **prolateral edge carina** toward the apex of the cheliceral fingers (fig. 6C, pl. 5C). A slight broadening at the base of the fixed finger between the two diverging rows of fondal teeth is termed the **fond** (Simon, 1879: 126, 1880: 402; Putnam, 1883: 257; Fichter, 1941; Muma, 1951). The fond is not synonymous with the **fondal notch**, present in many eremobatid males (see section on Size and Shape). The distal part of each finger is termed the **mucron** (Maury, 1970), redefined here as the part of the fixed finger distal to the distal tooth (FD), and the part of the movable finger distal to the medial tooth (MM), as measured from the notch of the tooth directly distal to FD or MM, to the terminal tooth (FT and MT; tip of finger). The mucra are usually toothless, but subterminal teeth are present on the mucron in some taxa (e.g., pl. 22D). Although the position of FD and MM can often be approximated, when absent, by comparison with related taxa, this is not always possible, and the proximal margin of the mucron is therefore often neither identifiable nor deducible when FD is absent.

The movable finger articulates ventrally with the fixed finger (figs. 1, 2, pl. 2) via a circular opening (Roewer, 1934: fig. 48), referred to here as the **interdigital foramen**, at the base of the fixed finger. The foramen is flanked distally by the fond, and demarcated by the **basal fondal margin**, bearing small to reduced **basifondal (BF)**

TABLE 5

Synonyms for cheliceral fingers of Solifugae used in the literature

Cheliceral finger	Dorsal/fixed finger; ventral/movable finger	Reference
	article cubital (d); *article digital mobile* (f)	Savigny (1809: 178, pl. 8, fig. 1c)
mors [jaw]	*mors immobile*	Dufour (1861)
jaw	*Unbeweglichen Kinnladen* [immovable jaw]; *Unterkiefer*	Koch (1842)
jaws	upper/dorsal jaw[a]; lower/ventral jaw	Pocock (1895); Purcell (1899: 393); Hewitt (1913, 1919b); Hirst (1916); Lawrence (1927); Lamoral (1972)
Kinnlade [jaw]	*obere/untere Kinnlade*	Birula (1929b: 279, fig. 5)
crochet [fang]	*crochet fixe en dessus/supérieur; crochet mobile/inférieur*	Simon (1872, 1879: 126, 1880)
fang	apophysis of penultimate[a, b] segment; terminal segment/fang	Pocock (1893: 10)
fang	upper/immovable fang; lower fang	Birula (1915: 4, 1916: 73)
dactylus/digit	upper digit/immovable dactylus; lower/movable digit	Pocock (1895, 1889)
digit	fixed digit; movable digit	Turk (1960); Levy and Shulov (1964)
digitus	*digitus fixus/immobilis; digitus mobilis*	Roewer (1934: 53); Klann (2009); Klann and Alberti (2010); Van der Meijden et al. (2012)
fingers	upper/fixed finger; lower/movable finger	Putnam (1883: 255–257); Banks (1900); Hewitt (1912); Muma (1970b)
Oberkieferfinger [maxillary finger]	*dorsaler/ventraler Oberkieferfinger*	Kraepelin (1899)
Mandibularfinger (Mdbfgr.)	*dorsale/unbewegliche Mandibularfinger; ventraler Mandibularfinger*	Kraepelin (1901)
doigt [finger]	*l'article basilaire*[a]*/doigt fixe, doigt mobile*	Sørensen (1914); Panouse (1960b)
Chelicerenfinger/digitus	*dorsalen unbeweglichen Chelicerenfinger; ventralen beweglichen Chelicerenfinger*	Roewer (1934: 53)
Finger, Oberkiefer	*Oberfinger/Oberkiefer; Unterfinger/Beweglicher Finger*	Birula (1937a)
dedo [finger]	*dedo immóvil; dedo móvil*	Mello-Leitão (1938); Maury (1970); Armas (1994)
finger	*fixed finger/movable finger*	Petrunkevitch (1955: 154); Selden and Shear (1996); Botero-Trujillo (2014)
finger	immobile/fixed finger; mobile finger	Klann (2009)
ramus/podomere	fixed ramus (FI)[a]; free ramus (FR)	Dunlop (2000)

[a] Use of "penultimate segment" (Pocock, 1893: 10), "upper jaw" (Hewitt, 1919b: 33), *l'article basilaire* (Sørensen, 1914: 158), and "fixed ramus" (Dunlop, 2000: 69) referred to paturon, i.e., included both fixed finger and manus.

[b] Pocock (1893) interpreted chelicera as three-segmented structure: lateral lobe of propeltidium as first segment, manus and upper finger as second or "penultimate" segment, and movable finger as third or "terminal" segment.

teeth in some taxa. **Interdigital articular membranes (iam)** connect the fixed and movable fingers, and permit articulation (Van der Meijden et al., 2012). The membrane visible in the fondal area is referred to here as the **fondal interdigital articular membrane (fiam)** and the membrane connecting the movable finger ventrally with the manus as the **ventral interdigital articular membrane (viam)**. The viam is flanked on each side by a sclerotized asetose area, probably serving for muscle or ligament attachment, at the base of the movable finger (**ventral digital plagula**, or **vdp**), and on the manus (**ventral manus plagula**, or **vmp**). The vmp terminates at each end in a distinct, rounded, and strongly sclerotized, external articulation sclerite (Muma, 1985), referred to respectively as the **pro-** and **retrolateral interdigital condyli** (**pic** and **ric**), articulating into the **pro-** and **retrolateral interdigital sockets** of the movable finger. These condyli together form a ventral bicondylar hinge through which the movable finger articulates with the fixed finger. The bicondylar hinge restricts movement of the fingers to the dorsoventral plane, allowing the teeth to overlap like scissors (Kraepelin, 1901) and transforming the chelicerae into the powerful offensive and defensive appendages they are (Roewer, 1934: 54). The two **interdigital condyli** determine the rotation axis of the fingers (Van der Meijden et al., 2012). The movable finger naturally closes prolateral to the fixed finger but may be forced to close retrolateral to it artifactually (pl. 94C).

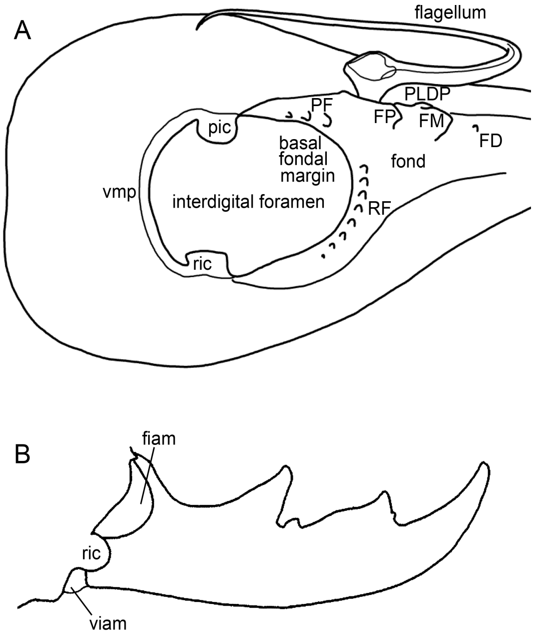

FIG. 2. Hexisopodidae Pocock, 1897 (**A**) and Daesiidae Kraepelin, 1899 (**B**), cheliceral interdigital articulation and attachment sites, illustrating condyli and articular membranes. **A.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795), paturon, ventral view, illustrating row of beadlike denticles at base of fond. **B.** *Biton* (*B.*) sp., ♂ (NMNW), Namibia: Windhoek, Auas Mountains, movable finger, retrolateral view. Abbreviations: **FD,** fixed finger, distal tooth; **fiam,** fondal interdigital articular membrane; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **PF,** profondal teeth; **pic,** prolateral interdigital condyle; **PLDP**, prolateral dental process; **RF,** retrofondal teeth; **ric,** retrolateral interdigital condyle; **vdp**, ventral digital plagula; **viam,** ventral interdigital articular membrane; **vmp,** ventral manus plagula.

The chelicera articulates basally with the propeltidium (fig. 3, pls. 1, 3). The opening through which the chelicera connects internally with the rest of the prosoma is referred to here as the **cheliceropeltidial foramen**. At the external margins of the chelicera, the exoskeleton is markedly bent inward to form a broad collarlike **basal cheliceral apodeme** that surrounds the foramen. The basal apodeme projects retrolaterally to form a sclerotized protuberance, the **cheliceropeltidial condyle (cpc)**, which articulates with the propeltidium of the prosoma to form an anterolateral cheliceropeltidial articulation (chelicerocarapacal articulation sensu Shultz, 1990) situated within the **anterolateral propeltidial lobe** (pls. 1A, 3A, B; Roewer, 1934: 32). The articulation site is often visible on the external surface of the propeltidial lobe as a pale area, the **external cheliceropeltidial condylar attachment (ecpca)**. A **cheliceropeltidial articular membrane (cpam)** connects the chelicera to the prosoma. This membrane is fixed to the chelicera along the margin separating

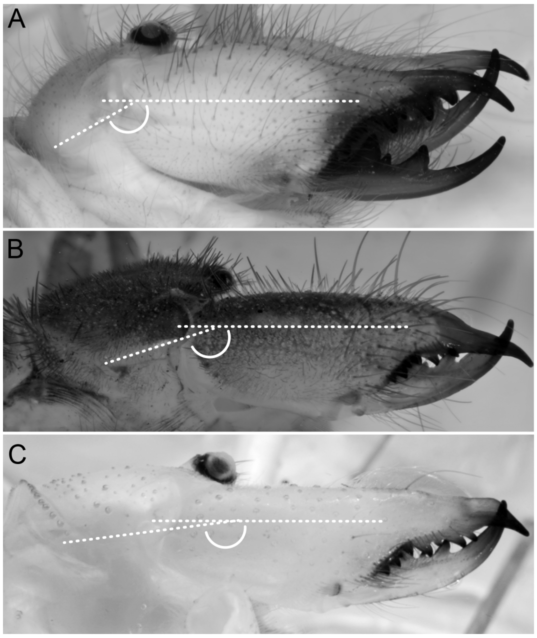

FIG. 3. Solpugidae Leach, 1815 (**A**), Daesiidae Kraepelin, 1899 (**B**), and Ammotrechidae Roewer, 1934 (**C**), cheliceral attachment to propeltidium, lateral views, illustrating increasingly obtuse angle formed between ventral margin of anterolateral propeltidial lobe and chelicera. **A.** *Zeria lawrencei* (Roewer, 1933), ♀ (NMNW 13820). **B.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **C.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]).

the external chelicera from the basal apodeme, thus forming a membranous collar around the basal apodeme and foramen. Sections of this membrane are prominent and clearly visible anterior to the propeltidial lobe, and ventral to the propeltidium and ocular tubercle in intact specimens (pl. 1A).

Size and Shape

Measurements: Solifuge chelicerae are often markedly sexually dimorphic. Although the absolute size and shape of the chelicera and its relative dimensions (e.g., aspect ratios and relative finger lengths) are sexually dimorphic (fig. 4), these metrics are often difficult to quantify. When measurements are presented in the solifuge literature, they are usually dimensions of length and height (depth) of the chelicera, although width (breadth) is occasionally included (e.g., Maury, 1980a). With few exceptions (e.g., Maury, 1980a; Botero-Trujillo, 2014), the terms “width” (e.g., Muma, 1951; Brookhart and Muma, 1981; Vázquez and Gaviño-Rojas, 2000; Peretti and Willemart, 2007; Catenazzi et al., 2009) and “breadth” (Cloudsley-Thompson, 1961) are traditionally used to describe the vertical axis of the chelicera in the solifuge literature. In the present contribution, following Maury (1980a) and Botero-Trujillo (2014), and in accordance with common usage in other taxa, e.g., scorpion pedipalp chela (Stahnke, 1970; Sissom and Francke, 1985) and crustacean cheliped propodus (Gregati and Negreiros-Fransozo, 2007), “height” is applied for the measure of the vertical axis and “width” (traditional “breadth”) reserved for the horizontal axis measured in dorsal view (fig. 5).

Ratios: Various indices exist to quantify cheliceral shape (fig. 5). The “jaw index” of Cloudsley-Thompson (1961: 149) calculates the aspect ratio of the chelicera (length/height), which Cloudsley-Thompson (1961) reported as larger in males than females, a general trend across the Solifugae, based on data from others (e.g., Panouse, 1960b; Punzo, 1998b; Peretti and Willemart, 2007). This ratio, referred to here as the **CL/CH** ratio (fig. 5D), is synonymous with the L/W (length/width) ratio of Brookhart and Muma (1981) and the CL/CW index of Vázquez and Gaviño-Rojas (2000). The **CL/CW*** ratio (length/width) (fig. 5E), newly proposed in the present contribution, and indicated with an asterisk to distinguish it from previous historical usage, similarly measures the relative volume of the chelicera. Higher CL/CH and CL/CW* ratios do not indicate a larger chelicera, but a less voluminous (robust) chelicera (fig. 4). The CL/CH (traditionally referred to as CL/CW) ratio and newly defined CL/CW* ratio thus quantify sexual dimorphism in cheliceral dimensions (gracile, narrower, in males and robust, broader in females), rather than which sex has the larger chelicera relative to body size. Note that the CL ("cheliceral line") of Punzo (1998a: 228, fig. 7–13A) should not be confused with CL for cheliceral length (in the present contribution).

According to Punzo (1998a), the **A/CP** ratio (Brookhart and Muma, 1981) is a more precise comparative measure of cheliceral size between sexes than the jaw index, or CL/CH ratio. However, the A/CP index (fig. 5F) was never intended to compare cheliceral sizes as it quantifies the ratio of appendages (A = sum of the lengths of pedipalp, leg I, and leg IV) to body length (CP = sum of the lengths of chelicera and propeltidium), not the ratio of cheliceral length to part of body length. Long-legged species present a higher A/CP value than short-legged species. The A/CP ratio is, therefore, inadequate for comparing relative cheliceral sizes between sexes because cheliceral length is included within the "body length" measurement that is compared to the length of noncheliceral appendages, which are typically longer in males than females. A/CP values are thus expected to be higher for males. In addition, the A/CP ratio can be used to distinguish between long-legged and short-legged species. Brookhart and Muma (1981: 286) found the A/CP ratio to be a reliable species indicator for both sexes. Muma (1951) initially included the opisthosoma in the calculation of total body length, but it was subsequently omitted (Brookhart and Muma, 1981, 1987; Muma and Brookhart, 1988) due to the capacity of the opisthosoma to greatly extend when engorged or gravid.

Two-dimensional measurements (cheliceral length, height and width) provide indications of variation within the sexes, and absolute differences between the sexes (e.g., smaller cheliceral length in males found by Punzo, 1998b), but fail to account for sexual dimorphism in body size. A relatively smaller (measured in absolute size) male chelicera may be an artifact of smaller body size. Peretti and Willemart (2007: 32, 33) reported larger chelicerae in males, but this was based on an erroneous interpretation of their aspect ratio values; a higher aspect ratio in males does not indicate larger chelicerae in males, but a *relatively* higher aspect ratio in females due to the larger denominator in the latter. Van der Meijden et al. (2012: 3412) mentioned that rhagodid males are smaller than females but that their chelicerae are "much larger" than those of females, whereas male Galeodidae Sundevall, 1833, "generally do not have enlarged chelicera" but failed to quantify these statements. Geometric morphometric analyses would provide a better indication of the relative proportions of male and female chelicerae across the order.

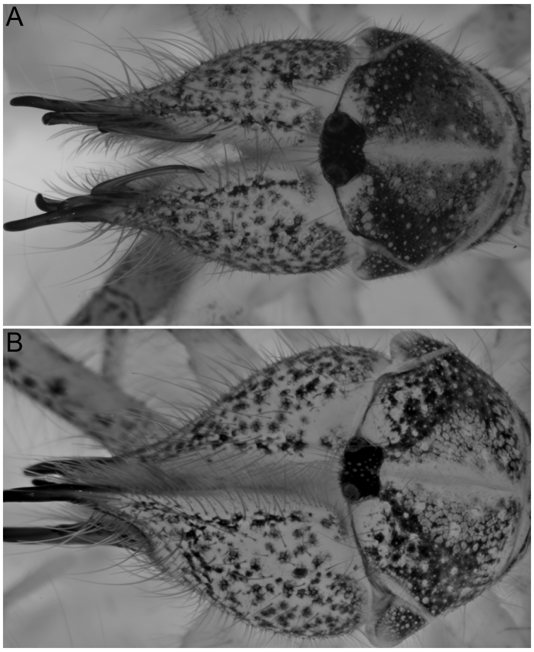

FIG. 4. Daesiidae Kraepelin, 1899, *Ammotrechelis goetschi* Roewer, 1934, chelicerae and propeltidium, dorsal views, illustrating sexual dimorphism (more gracile chelicera in ♂ than ♀). **A.** ♂ (AMNH [LP 10673]). **B.** ♀ (AMNH [LP 10673]).

Several eremobatid-specific ratios (fig. 5H) have been proposed (Brookhart and Muma, 1981, 1987; Muma and Brookhart, 1988; Punzo, 1998a: 228, figs. 7–13A; Brookhart and Cushing, 2002, 2004: 285, fig. 2), including the **FNL/FNH** (fondal notch length/fondal notch height) ratio, the **FNH/FFH** (fondal notch height/fixed finger height) ratio, and the **CH/FFH** (chelic-

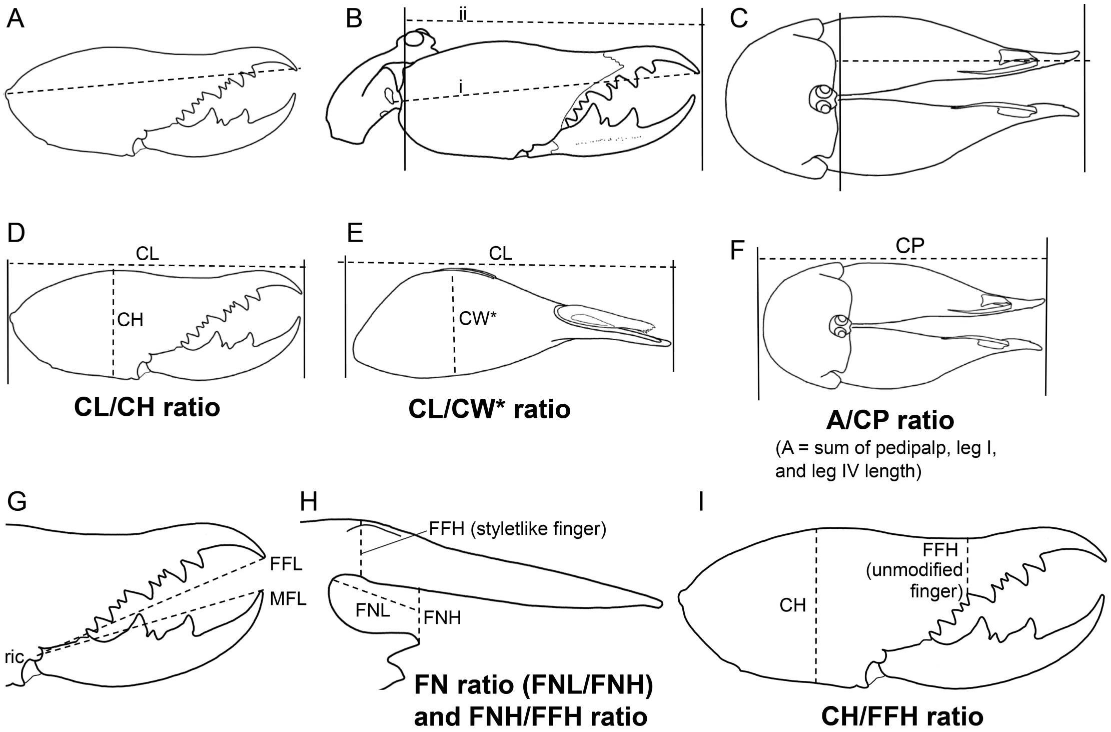

FIG. 5. Solifugae, chelicerae, retrolateral (**A, B, D, G, I**) and dorsal (**C, E, F**) views, and fixed finger, retrolateral view (**H**), measurements, ratios, and landmarks. **A–C.** Landmarks used to measure cheliceral length (CL), including (**A**) fixed finger apex to cheliceropeltidial condyle (Muma, 1951; Brookhart and Cushing, 2004); (**B**) fixed finger apex to anterolateral propeltidial lobe anterior margin, in direct line (i) or parallel to longitudinal axis (ii) of chelicera; and (**C**) fixed finger apex to propeltidium anterior margin. **D.** CL/CH ratio (Cloudsley-Thompson, 1961). **E.** CL/CW* ratio (asterisk indicates use of CW as defined in present contribution). **F.** A/CP index (Brookhart and Muma, 1981, 1987; Muma and Brookhart, 1988). **G.** Fixed and movable (ventral) finger lengths from retrolateral interdigital condyle (ric) center to (applicable) finger apex. **H.** FN ratio (FNL/FNH), i.e., fondal notch L/W or FN ratio sensu Brookhart and Muma (1981, 1987) and Muma and Brookhart (1988), and FL/FW ratio sensu Brookhart and Cushing (2004); and FNH/FFH ratio (FW/FFW) sensu Brookhart and Cushing (2004), based on finger to notch ratio (FF/FN) of Brookhart and Muma (1987), with numerator and denominator switched. **I.** CH/FFH ratio. Abbreviations: **CH,** cheliceral height; **CL,** cheliceral length; **CP,** chelicera-propeltidium length; **CW,** cheliceral height; **FFH,** fixed finger height; **FFL,** fixed finger length; **FN,** fondal notch; **FNH,** fondal notch height; **FNL,** fondal notch length; **MFL,** movable finger length; **ric,** retrolateral interdigital condyle.

eral height/fixed finger height) ratio. The latter was introduced by Brookhart and Cushing (2002: 84; their CW/FFW and CW/WFF ratios) to provide measurements for "species in which the fondal notch was absent or obscure," such as *Hemerotrecha cornuta* Brookhart and Cushing, 2002 (pl. 79I, J). The CH/FFH ratio is a useful indicator for species that exhibit an abrupt narrowing of the fixed finger, as in the species examined by these authors. Catenazzi et al. (2009: 151), citing Brookhart and Cushing (2002), suggested that width (or "height" as defined above) should be measured at the "base of the finger" in species without a fondal notch, but did not provide measurements and, as far as can be determined, the CH/FFH ratio has been calculated only in species that exhibit abrupt narrowing of the fixed finger. There is no reason why the CH/FFH ratio should not be applicable to conserved cheliceral shapes, provided the points of measurement (landmarks) are specified and consistently applied. Given that the modified eremobatid fixed finger broadens from a styletlike shape, directly proximal to the proximal tooth (FP), this point is the most appropriate landmark for FFH measurements in chelicerae with conserved shapes (fig. 5I).

Other measurements used on solifuge chelicerae include: (1) the length of the space occupied by the teeth on the movable finger, measured from the apex of the proximal tooth (MP) to the apex of the medial tooth (MM) (Muma, 1951: 122), and (2) the length of the **retrodorsal process (RDP)** on the fixed finger relative to the length of the fixed finger in male specimens of the *palpisetulosus* group of *Eremobates* (Muma and Brookhart, 1988). Muma and Brookhart (1988) also described the relative placements of the retrodorsal process.

LANDMARKS: The shape of the chelicera and the manner of its attachment to the propeltidium hinder the identification of unambiguous landmarks for recording measurements, often resulting in subjectivity. Height and width of the cheliceral manus or finger are measured as the distance between the furthest points (fig. 5A, B), and length of the fondal notch as the maximum distance within the fond (fig. 5H). Cheliceral shape determines the highest point of the chelicera. For example, Muma (1951) measured height across the manus in Eremobatidae and across the base of the movable finger in Ammotrechidae. The line of measurement for cheliceral length is also ambiguous. Pocock (1895: 78, footnote) measured the retrolateral side from the "point of articulation to the apex of the immovable **fang**." Purcell (1899: 407) also measured "apex to hinge." A similar measurement was applied to Eremobatidae by Muma (1951) and Brookhart and Cushing (2004: 285, fig. 2). Muma (1951: 40) clarified that this was conducted "in such a manner that the line of measurement was always within the chelicera" and when "the fixed finger was bent or curved, stadia permitting the longest line of measurement were utilized." It is unclear how this was achieved. A caveat of using the basal articulation as a landmark is that the chelicera has to be removed from the prosoma with the cheliceropeltidial condyle intact (fig. 5A) or the articulation point must be approximated, e.g., from the external cheliceropeltidial condylar attachment (ecpca). The latter is usually visible on the anterolateral propeltidial lobes (pls. 1A, 3A, B). Three alternatives would be to measure retrolaterally in a direct line from the fingertip to the anterior margin of the cheliceropeltidial lobe (fig. 5B, line i); retrolaterally in a line parallel to the cheliceral axis from the fingertip to the anterior margin of the cheliceropeltidial lobe (fig. 5B, line ii); or dorsally from the fingertip to the anterior margin of the propeltidium (fig. 5C). The third metric was found to be easiest in intact specimens, but not in specimens from which the chelicera was removed. The former (fig. 5B, line i) is recommended in the present contribution because of its utility in both attached and removed chelicerae. As the axis of measurement used may yield different measurements of length, consistent, standardized landmarks are imperative for repeatability and comparison among studies.

Statements concerning the relative lengths of the fixed and movable fingers (e.g., Wharton, 1981: 40; Hrušková-Martišová et al., 2010a) are subjective when the landmark defining the start of the fixed finger is arbitrarily defined. The interdigital condyli, which represent the start of the fixed finger, are proposed here as an unambiguous landmark for measuring the length of the fixed and movable fingers (condyle-to-fingertip line; fig. 5G). This landmark also accounts for the rotation axis that affects how the fingertips close relative to one another.

SHAPE: Most modifications in shape concern the fixed (dorsal) finger that, in some species, is elaborately to bizarrely modified in adult males (fig. 6, pl. 137). An upturn in the finger (pl. 67A), referred to as the **fixed finger crimp** (Brookhart and Cushing, 2004: 294, fig. 31), is common in

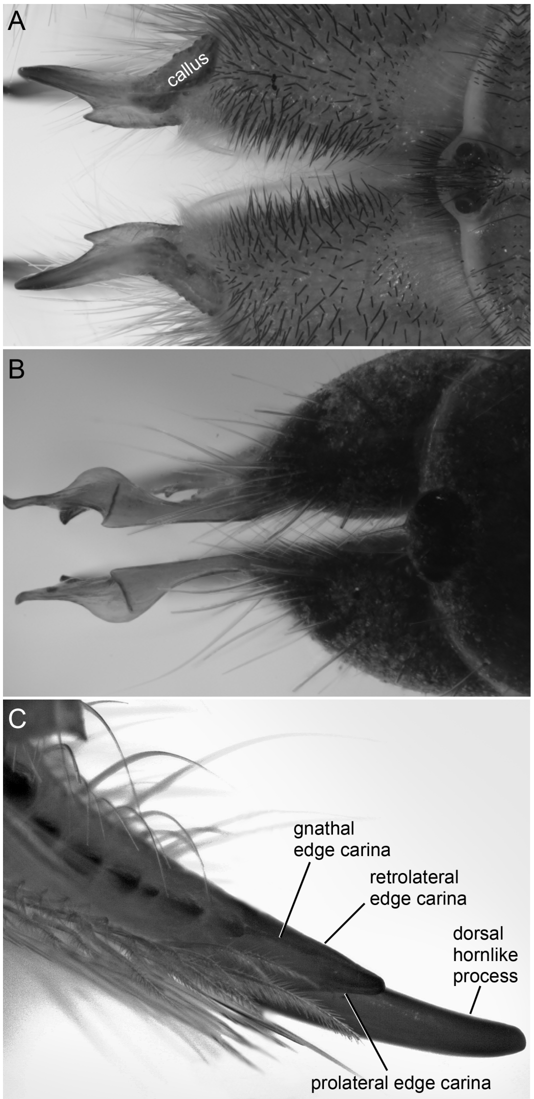

FIG. 6. Hexisopodidae Pocock, 1897 (**A**), Melanoblossiinae Roewer, 1933 (**B**), and Lipophaginae Wharton, 1981 (**C**), modified cheliceral fixed (dorsal) finger apices, dorsal (**A, B**) and ventral (**C**) views. **A.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426), illustrating callus, distinct asetose area on fixed finger. **B.** *Melanoblossia* sp., ♂ (AMNH [LP 9857]). **C.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]).

male eremobatids with a **styletlike fixed finger**. A broad, basal notch, or **fixed finger basal notch**, visible in dorsal view, characterizes species belonging to the *scaber* group of *Eremobates* (Muma, 1951; Brookhart and Cushing, 2004: 285, fig. 1). Modifications in males may include **dorsal hornlike processes** in Karschiidae, *Ammotrechelis goetschi* (Daesiidae), and *Trichotoma michaelseni* (Lipophaginae) and toothlike, proximodorsally to dorsally projecting, apically pointed spines, referred to as **dorsal cheliceral spines**, in some Daesiidae and *Karschia* (Karschiidae). Whereas the fixed finger is usually unmodified in adult females and immatures, an elevated crest, situated dorsally on the fixed finger and referred to as a **dorsal crest**, is common among adults and immatures of both sexes in Ammotrechidae, some Ceromidae, *Hemiblossia* (Daesiidae), and Mummuciidae (pls. 149E–H, 151C–F, 152B, C; “dorsal keel” of Botero-Trujillo, 2014: 321, 325, fig. 16). The dorsal crest may be pronounced and angular in females and immatures (i.e., the “dorsal hump” of Iuri et al., 2014: 21; Botero-Trujillo, 2014: 321, 325, figs. 11, 17; also see Muma, 1951: 124, 126, figs. 289–262, 272, 273).

Modifications of the movable (ventral) finger tend to be less pronounced but may involve slight differences in dentition or shape toward the apex (mucron) including, e.g., varying degrees of concavity, or a sudden narrowing at the apex to form a **ventral notch (VN)** (fig. 7B; Muma and Brookhart, 1988). The mucron of the fixed finger is usually more slender in males, and may be more markedly hooked, bent, or angular (e.g., *Karschia*, males in pl. 50) or less strongly curved (e.g., Galeodidae, males in pl. 62). Supra-generic trends are evident in cheliceral shape, e.g., a narrow chelicera is common in Ammotrechidae (pl. 146), a robust chelicera in Dinorhaxinae (pl. 56B), Hexisopodidae (pl. 129) and Rhagodidae (pl. 56C–H), and a narrow chelicera, often with long fingers, in Melanoblossiinae (pl. 154). Another recurrent pattern is the “eremobatid shape,” which comprises a prominent, vertical fond and a fixed finger shaped like a stylet for most of its length, with or without a **fondal**

notch separating the finger from the fond (fig. 7A, B). Similar shapes are evident, albeit often to a lesser degree, in other solifuge families, including Ceromidae (pl. 91H), Daesiidae, e.g., *Biton* (*B.*) *subulatus* (Purcell, 1899) (Kraepelin, 1901: 93, fig. 62), Gylippinae (pl. 85B), Karschiidae (pl. 50A), and Lipophaginae (pl. 87H).

Several taxa exhibit distinct gaps (notches or diastemas) between teeth (fig. 7). The fondal notch (FN) is situated proximal to the **fixed finger proximal (FP) tooth** of the median series (fig. 7A, B). It is usually toothless, although **denticles** are present in some eremobatid species (pl. 2B). A diastema within the median series, referred to here as the **medial notch (MN)**, is a toothless area between the **fixed finger medial (FM) tooth** and the **fixed finger submedial (FSM) tooth**, the latter always situated close to, or on the distal edge of the fixed finger proximal (FP) tooth in the presence of a diastema (fig. 7C, D). A medial notch is most prominent in Solpugidae, and is a diagnostic character for *Solpugema* Roewer, 1933 (Roewer, 1934: 420). Similarly positioned, but less pronounced toothless spaces occur in other Solpugidae, e.g., *Solpugista hastata* (Kraepelin, 1899), some Ammotrechidae (fig. 7D) and, apparently, Karschiidae (Roewer, 1934: 143, fig. 141C). Because the fondal notch is situated proximal to the median series, whereas the medial notch is situated within the median series, these toothless areas are unlikely to be homologous (fig. 7). The medial notch and the dentition associated with it are further discussed below.

Functional Morphology of Chelicerae

Mating Behavior: As discussed above, the chelicerae play a major role in the mating behavior of solifuges, cheliceral functionality in large part determining their size and shape (e.g., Hrušková-Martišová et al., 2010a; Van der Meijden et al., 2012). For example, Van der Meijden et al. (2012) speculated that a reproductive function (e.g., male-male antagonism) may explain the apparently larger chelicerae reported for male Rhagodidae (although this was not quantified). Others (e.g., Hrušková-Martišová et al., 2010a) suggested that cheliceral shape may be adapted for direct involvement in copulation.

The fixed finger of males is the part of the chelicera most involved in mating. The male flagellum originates on the fixed finger, and the finger may be modified in general size and shape, as well as in the shape of the mucron. Modifications of the movable finger are relatively rare and include a dorsally concave mucron, more pronounced in males of some taxa, e.g., *Namibesia pallida* Lawrence, 1962 (pls. 132A, 133A) and *Trichotoma michaelseni* (pls. 87A–D, 88A). The functional significance of modifications to the fixed and movable fingers are mostly unknown, but some possibilities can be suggested based on a few species in which mating has been reported.

The relative length of the cheliceral fingers in males, and specifically a shorter fixed (dorsal) finger, may be of functional significance when the movable finger holds, or kneads, the outside of the female's body in the area of the genital operculum while the fixed finger remains inserted in the female's gonopore (table 2). However, no such correlation appears to exist for the two species in which this behavior was reported (Hrušková-Martišová et al., 2010a; Peretti and Willemart, 2007). A marked difference in the length of the fingers is evident in *Gluvia dorsalis* (Latreille, 1817) (pl. 132I, J) but not in *Oltacola chacoensis* Roewer, 1934. Furthermore, the relative length of the fingers is difficult to quantify, emphasizing the need for standardized measurements, which are based on unambiguous landmarks and account for the axis of rotation.

The shape of the fixed finger is probably important for its insertion into the female reproductive tract. The fixed finger was observed to be inserted into the female reproductive tract in representatives of Ammotrechidae (Peretti and Willemart, 2007), Daesiidae (Hrušková-Martišová et al., 2010a), Eremobatidae (Muma, 1966b) and Galeodidae (Hrušková-

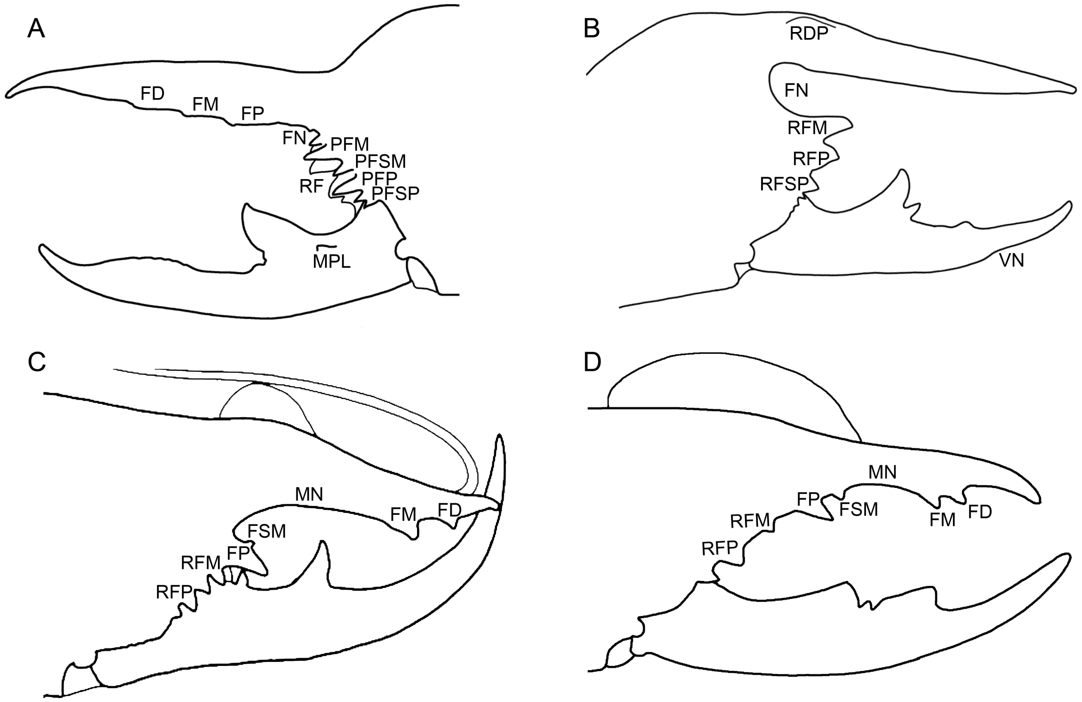

FIG. 7. Eremobatidae Kraepelin, 1899 (**A**, **B**), Solpugidae Leach, 1815 (**C**), and Ammotrechidae Roewer, 1934 (**D**), cheliceral shape modifications and positional comparison of fondal notch and medial notch, prolateral (**A**) and retrolateral (**B–D**) views. **A.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH), shallow fondal notch, illustrating proximal position, relative to reduced median series dentition. **B.** *Eremobates bajadae* Muma and Brookhart, 1988, ♂ (AMNH [LP 5740]), deep fondal notch. **C.** *Solpugema derbiana* (Pocock, 1895), ♂ (AMNH [LP 7709]), illustrating medial notch situated within median series dentition, distal to FP. **D.** *Branchia angustus* Muma, 1951, ♂, adapted from Muma (1951: 136, fig. 305), illustrating medial notch situated within median series dentition. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FN,** fondal notch; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MN,** medial notch; **MPL,** movable finger, prolateral tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **RDP,** retrodorsal process; **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; **VN,** ventral notch.

Martišová et al., 2008a, 2010a) (table 2), but how deep the fingers are inserted (e.g., most of the finger or only the mucron) is unclear due to differing interpretations regarding the proximal limit of the fixed finger. The narrow, tapering shape of the fixed finger, combined with the presence of a fondal notch, may facilitate a "deep" insertion in Eremobatidae (Muma, 1966b: 347). The tapering finger of male eremobatids may also be an adaptation to enter and pass through the narrowing oviducts of eremobatid females (table 4).

The shape and intersection of the apices of the male cheliceral fingers have been suggested to be sexually dimorphic, functioning more effectively as "pincers" during mating (Peretti and Willemart, 2007). Intersection of the finger apices is not restricted to males (e.g., pl. 62D), however, and is probably widespread in solifuges, even in species with a styletlike fixed finger, e.g., *Lipophaga trispinosa* Purcell, 1903 (pl. 85H), for which pinching or gripping may appear challenging. Examples of recorded behaviors that may be relevant to mucron shape include clasping the female during initial contact, presumably to subdue or manipulate her (Peretti and Willemart, 2007), gripping the female genital operculum in preparation for insemination (Peretti and Willemart, 2007; Hrušková-Martišová et al., 2010a), dragging the female up a vertical surface for insemination (Cloudsley-Thompson, 1961), or closing the genital opening postinsemination (Heymons, 1902; Amitai et al., 1962). None of these behaviors was reported in Eremobatidae (Muma, 1966b; Punzo, 1998b), all species of which possess a very straight, apically pointed cheliceral fixed finger in the adult male. As observations suggest that sperm is deposited in the form of a viscous sperm droplet, regardless of the type of packaging (table 3), mucron morphology is assumed to play a role in picking up (Amitai et al., 1962; Wharton, 1987; Hrušková-Martišová et al., 2010a, 2010b, 2008a) or catching (Cloudsley-Thompson, 1961), and subsequently holding and inserting the sperm droplet into the female (Wharton, 1987). In all Eremobatidae observed to date, sperm transfer was direct and the chelicera never handled the sperm droplet (Muma, 1966b). This behavior correlates with the straight, styletlike fixed finger of eremobatids, a morphology that would appear to be suboptimal for such a task.

It is here suggested that modifications in the shape of the male chelicerae, especially the fixed finger, are adaptations for pre- and postcopulatory probing of the female genital area, rather than insemination. The fact that the chelicera is not used to pick up sperm in Eremobatidae may have freed the fingers for other purposes in this family. This hypothesis is supported by the observation that some of the most markedly sexually dimorphic species occur in Eremobatidae, the family with direct insemination. Unfortunately, the paucity of data concerning both morphology and mating behavior restricts further understanding of this matter. However, it is noteworthy that the “typical” eremobatid chelicera (e.g., pl. 65H), with a toothless, styletlike fixed finger, is observed in other, diverse families, suggesting the possibility of convergence due to similar mating strategies (e.g., pl. 85A). Another example of possibly convergent cheliceral morphology is the similarity in mucron shape in the ammotrechid, *Nothopuga cuyana* Maury, 1976 (pl. 146H) and the karschiid, *Karschia* (pl. 50B, F). A comparison and possible correlation among mating behavior, female genital anatomy, and similar male cheliceral morphology (e.g., similar cheliceral shapes in many species of *Biton* Karsch, 1880, pl. 143) may improve understanding of the functional morphology of the male chelicera, among both distantly and closely related taxa.

OTHER BEHAVIOR: Sexual dimorphism in shape is not necessarily linked only to mating behavior. Hrušková-Martišová et al. (2010a: 94) described the chelicerae of two species observed as “straighter” and more elongated in males than females, and inferred that this difference in shape might confer a benefit during insemination, in particular during the “contact phase.” Although supported by observations of insertion of the entire chelicera into the female reproductive tract during mating (Amitai et al., 1962), few reports of mating described insertion of an entire chelicera, although the male chelicera is generally more gracile across the order. Deconstructing sexual dimorphism in shape (fig. 4) suggests that the gracile appearance of the male chelicera is largely attributed to its straight fixed finger and shallower, narrower manus, whereas the robust female chelicera is largely attributed to its curved fixed finger and deeper, wider manus. The fixed finger of the male is commonly inserted into the female genital tract. As the manus contains the muscles that provide the bite force of the fingers required, e.g., to break the hard exoskeleton of prey, a more voluminous manus is expected to accommodate larger muscles in females with their voracious appetites. Conversely, reduced feeding and differences in prey preference have been reported in males (Junqua, 1962; Wharton, 1987). For example, male *Gluvia dorsalis* did not feed on sclerotized beetles in the laboratory, unlike conspecific females, which readily did so (Hrušková-Martišová et al., 2010b). It may therefore be concluded that the sexual difference in cheliceral manus volume is more likely the consequence of selection for improved predation ability, leading to a larger manus, in females, rather than selection for a smaller manus to assist males in mating.

The mechanical "bite force" of galeodid and rhagodid species was measured by Van der Meijden et al. (2012), who found the aspect ratio of the chelicera to be negatively correlated with bite force, which is higher in Rhagodidae, with low cheliceral aspect ratio, than in Galeodidae, with high cheliceral aspect ratio. Van der Meijden et al. (2012: 3417) also suggested that a low aspect ratio may be an adaptation to "reduce the risk of structural failure" of the chelicera when subjected to force, as might be experienced during burrowing by fossorial solifuges, e.g., Rhagodidae and Hexisopodidae. This suggestion is supported by evidence that fossorial rhagodids possess a greater bite force at the tips of the chelicerae than surface-living galeodids (Van der Meijden et al., 2012). However, a greater force strength was found over the **movable finger proximal tooth (MP)**, i.e., the "main tooth" of Van der Meijden et al. (2012), in Galeodidae, suggesting that galeodids might be less effective burrowers, but with a greater ability to crush sclerotized beetles, than rhagodids. It may therefore be possible to associate the shape of the chelicera of different solifuge families with their dietary preferences, but no other study to date has investigated the components of cheliceral morphology necessary to handle prey. A large body of research on the chela (claw) of the crustacean cheliped may offer parallel insights into the functions of solifuge chelicerae. For example, in Crustacea, robust chelae possess a higher pinch force, at the cost of a slower closure. Such chelae typically possess larger, more blunt-edged molars (teeth), whereas slender chelae with long, narrow fingers are typically weaker but faster, and possess smaller, sharper and more numerous molars (Taylor, 1999). Extending these observations to Solifugae, the slender, **multidentate** chelicerae of the small Melanoblossiinae (pl. 154), for example, might be adapted for speed rather than force in catching small, fast running prey, compared with the robust chelicerae of larger solifuge taxa.

Integument

Asetose Areas: The chelicerae of solifuges are covered in setae except in specific areas devoid thereof, referred to here as **asetose areas** (pls. 1B, C, 4). Large areas of the distal parts of the cheliceral fingers, extending along each finger and always including the teeth and gnathal edges, are asetose, as are the smooth and shiny **stridulatory plate**, bearing the **stridulatory ridges** (see section on Stridulatory Apparatus), the **interdigital condyli** and **ventral manus plagula (vmp)** at the ventrodistal end of the manus, and the similar **ventral digital plagula (vdp)** at the base of the movable finger that connects the sockets ventrally (pls. 2C, 6A). Asetose areas are usually well defined and heavily sclerotized (pl. 4). The distinctly demarcated dorsal margin of the asetose area of the fixed finger is situated directly dorsal to the row of **prodorsal distal (*pdd*) setae** and referred to as the **prodorsal distal margin (pddm)**. The ventral margin of the asetose area is situated directly ventral to the proventral distal (*pvd*) row of setae and referred to as the **proventral distal margin (pvdm)** (pl. 1C). In Hexisopodidae, the heavily sclerotized asetose area on the fixed finger is usually lobate dorsally and referred to as a **callus** (fig. 6A, pls. 127C, 128D, E; Wharton, 1981). The callus often possesses blunt spinelike processes, or tubercles. A small, round structure, paler than the surrounding cuticle, and situated prolaterally on the mucron, slightly distal to the fixed (dorsal) finger distal (FD) tooth, is referred to here as the **mucron organ** (**mo**). It was observed in female

Ammotrechidae, and in both sexes of Galeodidae (pl. 60A) and Solpugidae (fig. 24B, pl. 27E). Botero-Trujillo (personal commun.) observed it in mummuciid females and juveniles. The mucron organ is often difficult to detect, however, and its taxonomic distribution merits further investigation. It is commonly situated on a shallow elevation or a small, prodistally directed toothlike structure that is often combined with a distally directed, toothlike **flagellar groove process (FGP)** in Solpugidae (fig. 24B, inset). The function of the mucron organ is unknown.

Setae and structures derived from setae (e.g., the male flagellum) rarely originate within asetose areas and, if situated near the margins thereof, the sclerotized area usually curves around the base of these structures (pl. 4A–C). Apparent exceptions include the gylippine flagellum, which appears to originate on the asetose area of the fixed finger (pl. 4D), and the setae that occur in the fondal notch of many Eremobatidae (pl. 4F). However, the flagellum of Gylippinae is hypothesized to originate in the setose area, the basal part fused with and impossible to distinguish from the sclerotized section of the fixed finger, much like the shaft of the flagellum of Solpugidae, which is fused to part of the fixed finger (see section on Male Flagellum and Flagellar Complex). Closer examination of the setae apparently situated within the fondal notch of Eremobatidae (*rlf* in pl. 4F) reveals that the asetose area is still present, but somewhat displaced prolaterally, and reduced to a narrow strip that sometimes contains denticles (pl. 4E). Unlike setae, taxon-specific hornlike cheliceral processes and macrostructures (flanges, carinae, processes and toothlike projections), especially common in Solpugidae (e.g., pl. 20; also see section on Taxonomic Diversity of the Flagellar Complex), are restricted to the asetose areas of the fingers.

CANALS AND GRANULATION: Prominent narrow **cuticular canals**, extending approximately perpendicular to the axis of the finger and apparently traversing the width of the endocuticle to the surface, are usually visible through the cuticle of the asetose areas of solifuge cheliceral fingers (pl. 5A; Bernard, 1896; Hewitt, 1919b: 12; Roewer 1934: 118). The function of these canals is unknown. Hewitt (1919b) speculated that they may be sensory, but this is unlikely. So-called **granulations** (e.g., Lawrence, 1972: 99), situated on the asetose areas of the cheliceral fingers (pls. 1B, 5B, C), and arranged in a row along a low longitudinal carina (an extension of either the prolateral edge carina or the retrolateral edge carina, i.e., the retrolateral longitudinal carina), are most prominent on the retrolateral surface of the movable finger, but may also be present on its prolateral surface. A similar row of granules occurs on the fixed finger of some species. Less distinct granules, the functions of which are unknown, are often distributed randomly toward the apices of the fingers. Some of the canals visible through the cuticle terminate in these granules. Although the canals were reported to open externally through pores (e.g., Hewitt, 1919b), no external openings were observed in the present study (fig. 8). Bernard (1896: 232) suggested that the granules are setal pores ("pores of vanished hairs"), a hypothesis supported by the observation of "pores" (granules) that continue to transverse the finger distal to the apicalmost prolateral movable finger setae. Further support for this hypothesis is evident on the retrolateral surface, where a cluster of setae, referred to here as the **retrolateral proximal setal cluster (*rlpc*)**, is situated at the base of the row of granules (pls. 18, 19). Narrow canals, connecting to setae, are also visible on other parts of the chelicera, notably the retrolateral surface of the fixed finger. Females and juveniles possess similar granulation and, in some cases, even more prominent and/or extensive granulation than males, especially on the fixed finger (e.g., compare sexes in pls. 67B, D, J, L, 104B, D, 124B, D, 126B, G, 132B, D, 136F, H).

SENSE ORGANS: Hansen (1894: 178, pl. 3, fig. 6) identified two lyriform organs situated ventrally on the chelicera, near the interdigital articulation, one on the movable finger, slightly distal to the point of articulation, and the second on the manus, slightly proximal to the point of articulation (pl. 6A). Hansen (1894) described these depressions as consisting of a small number of canals flattening toward the surface to open to the outside via narrow fissures, each with a small central dilation. In the few taxa available for study, Hansen (1894) observed a slight change in the position of this organ on the manus, noting in particular its more prolateral position in *Galeodes*. Close to these structures, and reported here for the first time, is a series of less defined, round to oval depressions situated proventrally on the stridulatory plate, and referred to here as the **medioventral organ** (**mvo**) (pl. 6), distinctly visible as an irregular depressed area on the ventral margin of the stridulatory plate in Carvalho et al. (2010: 26, fig. 19). Although more distinct in some taxa than others, this organ appears to be present in both sexes of all species. The depressions comprising the medioventral organ are all situated on or near the ventral margin of the stridulatory plate, which is less clearly demarcated than its dorsal and distal margins. Closer inspection reveals the margin in many species to be largely irregular due to the presence of a few setae, which may be associated with the medioventral organ (see pl. 6B–D, arrows), situated dorsal to the ventral margin of the stridulatory plate.

A concentration of sense organs therefore occurs on the ventral surface of the chelicera in the area where the fingers articulate. The pedipalpal coxal gland is situated on the dorsal surface of the pedipalp coxa directly ventral to the chelicera. Although its precise function remains unknown, some suggestions were offered by Roewer (1934: 191, 192). The coxal glands present a distinct outer morphology comprising an anterodorsally directed papilla referred to by Buxton (1913: 253) as the nozzle and by Alberti (1979) as the *Mündungsapparat*. Associated with the nozzle, referred to here as the **coxal gland nozzle (cgn)**, are **coxal gland setae (*cgs*)** and **coxal gland nozzle seta/e (*cgns*)**, respectively situated anterior to and on the nozzle itself (pl. 7). The coxal gland opening is situated on the dorsal side of the nozzle at its base (Alberti, 1979). The form and location of the nozzle suggest that it serves as a conduit for channeling gland secretions toward the chelicera (pl. 7), as proposed by Buxton (1913). Some taxonomic variation was observed in nozzle morphology and in the number and directionality of the *cgs* and *cgns* setae associated with it. Regardless of such differences, however, the structure retained the anterodorsally directed orientation of the nozzle and coxal gland setae in all taxa examined. The morphology and position of the coxal gland therefore optimizes contact with the ventral chelicera. The palpal coxal gland is not discussed further in the present contribution because it is not part of the chelicera. A possible association with the sensory organs of the chelicera should be further investigated, however.

STRIDULATORY APPARATUS

TERMINOLOGY: Audible stridulation in solifuges, by rubbing the chelicera together, was reported by P.S. Pallas in the 18th century (Bernard, 1896). A smooth, well-defined area of ridges, situated on the prolateral surface of the cheliceral manus (pls. 1C, 8–10) was first documented by Dufour (1861: 393). Hansen (1894: 184) ascribed a stridulatory function to the "sharp keels" and "naked, shiny, square plane," and named it the *stridulatory apparatus*. Kraepelin (1899) used the term *stridulatory ridges* for the first time, and the surface on which these ridges are placed was later referred to as the *stridulatory area* (e.g., Hewitt, 1931) or *stridulatory plate* (Turk, 1960). Turk (1960) was the first to associate the modified setae distal to the stridulatory plate with the stridulatory apparatus, and referred to these as *stridulatory setae* (fig. 9; pls. 10, 11). Hrušková-Martišová et al. (2008b) suggested that a stridulatory apparatus consists of two identical files, one on each chelicera. In the present contribution, the stridulatory apparatus is defined as comprising stridulatory setae distal to a stridulatory plate with stridulatory ridges.

Morphology: The structure of the **stridulatory apparatus** varies among solifuge taxa. The **stridulatory plate** at the base of the manus is present in all Solifugae. The approximately parallel **stridulatory ridges** commonly found on the stridulatory plate do not cover the entire surface, but are concentrated dorsodistally. The extent to which the plate is covered by ridges, and their number and development, differ among taxa (figs. 23A, 24D, 26A, pls. 8, 9). Hansen (1894) was the first to compare the stridulatory ridges among families. The first SEM images of stridulatory ridges (an ammotrechid, a galeodid, and a rhagodid) were provided by Cloudsley-Thompson and Constantinou (1984), who summarized the family-level differences reported earlier by Hansen (1894). Based on the observations of Hansen (1894) and Cloudsley-Thompson and Constantinou (1984), SEM images provided by later workers (Hrušková-Martišová et al., 2008b; Carvalho et al., 2010; Erdek, 2010; Bayram et al., 2011; González Reyes and Corronca, 2013; Botero-Trujillo, 2014; Iuri et al., 2014), and material examined in the present study, the following family-level differences were identified.

Stridulatory ridges appear to be absent in Karschiidae (pl. 8A–C; Hansen, 1894). Short, well-developed ridges are arranged in a strip at the distal border of the stridulatory plate in Rhagodidae (pl. 10; Hansen, 1894; Cloudsley-Thompson and Constantinou, 1984: 367, fig. 2). Vestigial ridges with short distal corrugations occur in Galeodidae (Hansen, 1894; Cloudsley-Thompson and Constantinou, 1984: 366, fig. 1; Hrušková-Martišová et al., 2008b: 444, fig. 1). The ridges are well developed but relatively short and of similar length in Lipophaginae (fig. 23A) but very vague in Gylippinae (pl. 8D, E). Stridulatory ridges are also barely visible in Ceromidae (pl. 8F). Well-developed, parallel ridges cover the dorsodistal surface of the stridulatory plate in Solpugidae (fig. 24A, D, pl. 9A, B). A reticulation of fine ridges at the distal border of the stridulatory plate is all that is evident in Hexisopodidae (Kraepelin, 1901: 8; Hewitt, 1931; but see Purcell, 1899: 383). Well-devel-

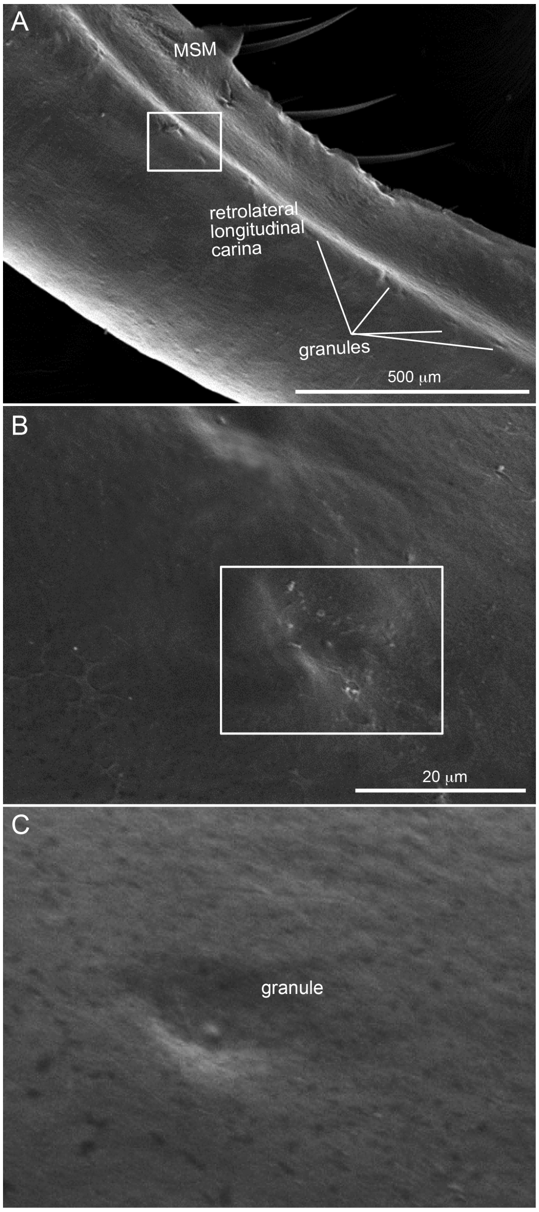

FIG. 8. Solpugidae Leach, 1815, *Solpugiba lineata* (C.L. Koch, 1842), ♂ (AMNH [LP 5919]), cheliceral movable finger, retrolateral view, illustrating granulation on retrolateral longitudinal carina (**A**), enlargement of individual granule (**B**), and close-up, illustrating apparent absence of external pore (**C**). Abbreviation: **MSM,** movable finger, submedial tooth.

oped, parallel ridges, the dorsal ridges of which are especially long, also occur in Ammotrechidae (Cloudsley-Thompson and Constantinou, 1984: 368, fig. 3; Iuri et al., 2014: 28, fig. 23), Mummuciidae (Carvalho et al., 2010: 25, 26, figs. 13, 19; González Reyes and Corronca, 2013: 541, figs. 4, 5; Botero-Trujillo, 2014: 325, figs. 10, 12), and Daesiidae (pl. 9C–F; Erdek, 2010: xlii, lxx, figs. 3.16, 3.48; Bayram et al., 2011: 125, figs. 3A6, B6). A few well developed ridges occur in Melanoblossiinae (fig. 26A). The ridges are less robust in Dinorhaxinae, but remain well differentiated, restricted to the dorsal half of the stridulatory plate, and approximately parallel to one another. Kraepelin's (1899) key distinguished between Daesiinae (current Daesiidae) and Dataminae (currently Eremobatidae) partly on the basis of the stridulatory ridges being well defined in daesiids and reduced or restricted to short ridges at the distal margin of the plate in eremobatids. Irregular areas in the ridges were noted in some Solpugidae, in apparently distantly related species (pls. 97A, 123A). Irregularities in *Biton* (*B.*) *zederbaueri* (Werner, 1905) (Daesiidae) were illustrated by Erdek (2010: xIii, figs. 3.16, 3.48) and Bayram et al. (2011: 126, fig. 6 A11). Irregularities were not observed in all specimens, suggesting they may have been caused by rubbing of the chelicerae (M. Erdek, personal commun.).

Stridulatory setae belong to the **promedial (*pm*) setal field**, the field of setae between the stridulatory plate and the **proventral subdistal (*pvsd*) setae** (pl. 10; see section on Chaetotaxy). These setae vary from unmodified to highly modified. Distinctly modified, regularly spaced stridulatory setae occur in Eremobatidae (fig. 9E, pl. 11E), Galeodidae (fig. 9A–C, pl. 11G–I), and Rhagodidae (fig. 9D, pls. 10, 11F). All distinctly modified stridulatory setae possess a swollen base, inserted or bent so they are distally directed, sometimes markedly so (e.g., Birula, 1925; Cloudsley-Thompson and Constantinou, 1984: 367, fig. 2c), and a thin, filamentous, and hairlike (acuminate) tip (fig. 9). The swollen base is a cuticular elevation of the socket in Eremobatidae, whereas the base of the seta itself is swollen in other families. The acuminate tip was found to "bear small forking branches" in *Galeodes granti* Pocock, 1903 (Cloudsley-Thompson and Constantinou, 1984: 366). Turk (1960) identified three main forms of stridulatory setae in Galeodidae, within which further variations were observed. Type I (*arabs* type) setae possess a swollen, rodlike base, which abruptly and asymmetrically transitions into a very long, very fine, filamentous hair (fig. 9A, pl. 11I; Birula, 1925: 191, fig. 3a; Turk, 1960: 112, fig. 1; Cloudsley-Thompson and Constantinou, 1984: 366, fig. 1b–d). Type II (*araneoides* type) setae possess a swollen, gradually tapering base, the tip of which transitions asymmetrically into a long filamentous hair (fig. 9B, pl. 11G, H; Birula, 1925: 191, fig. 3b; Turk, 1960: 114, fig. 2; Cloudsley-Thompson and Constantinou, 1984: 367, fig. 2b–c). Type III (*medusae* type) setae possess a laterally compressed base that gradually broadens until it abruptly narrows to a long filamentious hair offset asymmetrically from the flat base, from which the filamentous hair arises gradually and asymmetrically (Turk, 1960: 115, fig. 4, reproduced here in fig. 9C). The setae of rhagodids resemble galeodid type II setae (fig. 9D, pl. 11F). The extent to which the setae are capable of movement depends on the nature and extent of their swollen bases, as well as the angle of insertion (Cloudsley-Thompson and Constantinou, 1984). Birula (1925) was the first to call attention to the value of stridulatory setae in galeodid taxonomy. A detailed survey of the stridulatory setae and evaluation of their taxonomic significance is needed.

FUNCTION AND MECHANISM: Sound production is commonly reported for larger species of Solifugae (Hutton, 1843; Pocock, 1898, 1900a) but may be inaudible to the human ear or absent in smaller species (e.g., Punzo, 1998c). Hansen (1894) was the first to test the stridulatory function (sound production by friction) of the apparatus. By rubbing the chelicerae of a large specimen against one another, a sound reportedly audible up to 3 m was manually reproduced. Beyond these early investigations, the precise mechanism(s) of sound production remain little understood (Hrušková-Martišová et al., 2008b). Different forms of stridulatory setae may affect the type and amplification of sound produced. Hypotheses for sound generation were proposed by Dumortier (1964) and Cloudsley-Thompson and Constantinou (1984). These hypotheses involve sound production by scraping the stridulatory bristles over the stridulatory ridges of the opposite chelicera (Dumontier, 1964; Cloudsley-Thompson and Constantinou, 1984, for Rhagodidae), rubbing together the enlarged, relatively ridged bases, and amplifying the resulting sound with vibrations of the long, filamentous hair (Cloudsley-Thompson and Constantinou, 1984, for Galeodidae), or rubbing together well-developed ridges on opposing cheliceral surfaces (Cloudsley-Thompson and Constantinou, 1984, for Ammotrechidae). Hrušková-Martišová et al. (2008b: 440) suggested that intrageneric similarity in stridulatory apparatus morphology may produce genus-specific sounds, and intraspecific uniformity may reduce intraspecific "cannibalistic tendencies." Another hypothesis proposed by these authors is that solifuges might imitate those "acoustically aposematic organism[s]," such as vipers, with which they share a habitat (Hrušková-Martišová et al., 2008b: 447).

Hrušková-Martišová et al. (2008b) observed relative stability in the number and morphology of ridges among life stages, the length of ridges and the thickness of stridulatory setae increasing isometrically with body size in *Galeodes caspius subfuscus* Birula, 1937. These observations, in turn, correlated with similarities in the sounds produced at different life stages. Hrušková-Martišová et al. (2008b) concluded that the primary role of stridulation is defense, rather than intraspecific (i.e., intersexual) communication, a conclusion in accord with previous authors (Hutton, 1843; Pocock, 1898; Cloudsley-Thompson and Constantinou, 1984). Stridulatory ridges appear to be more

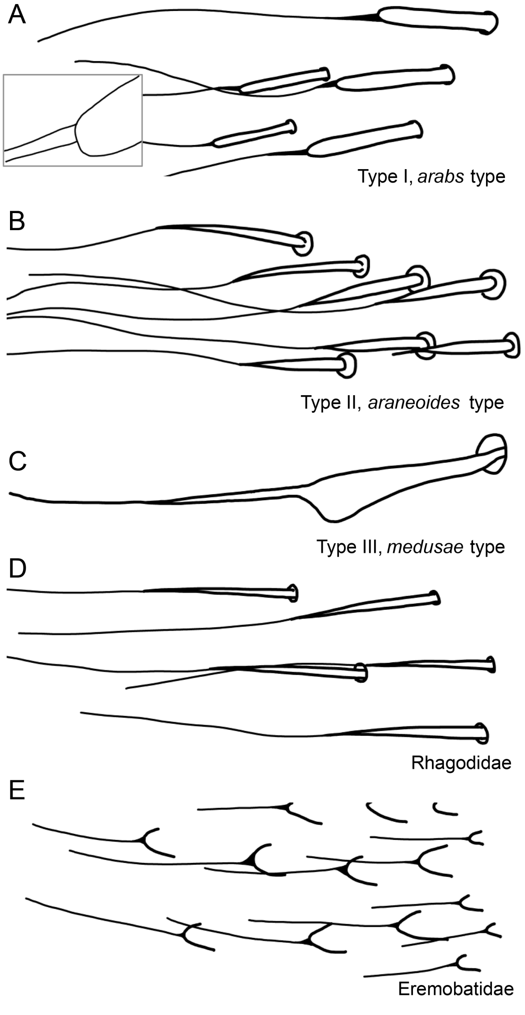

FIG. 9. Galeodidae Sundevall, 1833 (**A–C**), Rhagodidae Pocock, 1897 (**D**), and Eremobatidae Kraepelin, 1899 (**E**), modified cheliceral stridulatory setae. **A.** *Galeodes* sp., ♂ (AMNH [LP 11204]), type I (*arabs* type) setae. Inset: apex of setal base, adapted from Cloudsley-Thompson and Constantinou (1984: 366, fig. 1d). **B.** *Paragaleodes nesterovi* Birula, 1916, ♂ (AMNH [LP 7480]), type II (*araneoides* type) setae. **C.** *Galeodes medusae* Turk, 1960, ♂, type III (*medusae* type) setae, adapted from Turk (1960: 115, fig. 4). **D.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). **E.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]).

developed in nocturnal than diurnal taxa (Hewitt, 1919b), but this requires further investigation.

Unlike the stridulatory apparatuses of spiders and scorpions, which are quite varied in structure and position, solifuges possess only a single kind of stridulatory apparatus (Bernard, 1896; Dumortier, 1964). Stridulation might not be the only, or even the primary function of this structure in solifuges. Pocock (1897) and Hewitt (1919b) speculated that the ridges might serve a masticatory rather than a stridulatory function, at least in some species. The ridges are often slightly less developed (cf. males in pl. 9A, C with females in pl. 9B, D; Birula, 1913: 330; Hewitt, 1934) or absent (Hewitt, 1919b) in males compared to conspecific females. The grinding of food between the stridulatory ridges is included in the concept of the **cheliceral mill**, which refers to the combination of movements made by the chelicerae and cheliceral fingers during feeding (Lawrence, 1949a; Muma, 1966c). Prey is crushed into pulp in a combined scissors-and-saw movement, the former caused by the nature of the articulation between the two fingers, and the latter by an alternating forward and backward movement of the chelicerae (Bernard, 1897; Turner, 1916). Also associated with the chelicera is the rostrum (pl. 92A), which filters food through plates of anastomosed setae (sieves), and contains the mouth and pharynx. The rostrum is situated between the chelicerae in such a manner that the mouth at its tip is optimally positioned to receive liquid food and perhaps also masticated food particles (Muma, 1966c), flowing from the ridges. The possibility that the stridulatory apparatus may play a role in feeding, e.g., in grinding solid food and directing liquid food toward the mouth, is suggested by its weaker development in males, which seem to feed less than females (Junqua, 1962; Wharton, 1987). In conclusion, it is likely that the stridulatory apparatus possesses a dual feeding (masticatory) and stridulatory function. The latter may have evolved subsequent to the former, or vice versa.

Chaetotaxy

One of the most striking features of Solifugae is their extensive **chaetotaxy** (Lamoral, 1973) and the chelicerae are no exception. The only areas devoid of setae are the asetose areas described above (pls. 1B, C, 4). A full survey of cheliceral setation is beyond the scope of this contribution, but basic patterns of setal arrangement are discussed as no work on chelicerae is complete without setation, and because a discussion on the flagellum is impossible without an understanding of cheliceral chaetotaxy. In the present contribution, setae refer to **macrosetae**, large, dark, sclerotized socketed setae that may be spiniform (rigid) or setiform (flexible), as opposed to **microsetae**, which refer to small, pale, unsclerotized socketed setae. Spiniform macrosetae were traditionally referred to as "spines" in the solifuge literature. However, these structures are usually hollow, socketed processes, a typical setal morphology (Gorb, 2001), unlike **spines**, which are multicellular cuticular processes fixed immovably to the surface. True spines are rare in solifuges (Lamoral, 1973) and, on the chelicera, are restricted to the hornlike and toothlike cheliceral processes observed in species of *Eusimonia* (Karschiidae) (pls. 30D, 31B) and some Daesiidae, although, strictly speaking, the teeth also fit the definition of spines. Lamoral (1973: 86) suggested use of "spine-like setae" instead of "spine" for spiniform setae. The more precise term, spiniform macrosetae (or spiniform setae), is preferred in the present contribution. **Bifid setae** (fig. 10A) are common on the body and appendages of solifuges but, on the chelicera, are restricted to the setae categorized as **retrolateral setae**, including those situated prodorsally on the chelicera (i.e., the dorsal **retrolateral manus setae**, or ***rlm***) (pl. 14B), which may be of varying length and thickness. "Typical" **plumose setae** (fig. 10B) are restricted to the prolateral surface of the chelicera (proventral distal setae, or *pvd*; **movable finger prodorsal setae**, or ***mpd***; **movable finger fondal setae**, or ***mff***) and the lateral lips of the rostrum (lateral lip flagella, pl. 92A), areas closely associated with feeding. The dorsalmost of the retrolateral proximal setal cluster (*rlpc*) is weakly plumose in some species. Depending on the species, setal plumosity varies from symmetric to asymmetric, sparse to dense, and covers the distal third to four-fifths of the seta (e.g., Birula, 1913: 325, fig. 3a) or its entire length (e.g., Lawrence, 1968: 75, figs. 7b, e for *Trichotoma brunnea* Lawrence, 1968). Plumose setae are absent in male Hexisopodidae. Even fondal setae and the lateral lip flagella of the rostrum are, at most, striated in male hexisopodids. The plumose setae of male Rhagodidae tend to be restricted to a few setae close to the interdigital articulation.

Paturon Prolateral Surface: Setae on the prolateral surfaces of the chelicerae (**prolateral setae**) of both sexes are arranged in a distinct pattern (Carvalho et al., 2010: 36, fig. 19), comprising longitudinal series (rows) and fields of setae named in accordance with position and setal morphology (pls. 12A, 13, 14). This pattern is distinct in most, but not all taxa. Hexisopodidae represent the best example of the absence of such a distinct pattern. Hexisopodid males possess a largely homogeneous covering of setiform prolateral setae, except for slightly more stiff, robust proventral distal (*pvd*) setae (Hewitt, 1931) and a small field of short spiniform setae (**prodorsal spiniform setal cluster**, or ***pdsc***) prodistally on the fixed finger next to the callus in some *Chelypus* species, considered part of the male flagellar complex (pls. 32C, 33E, 130D). The cheliceral setae of Dinorhaxinae and Rhagodidae are also relatively uniform, but less so than those of Hexisopodidae. Birula (1913: 331, fig. 9) provided the most complete categorization of prolateral cheliceral setae, but covered only the most prominent setal groups. Based on placement and basic morphology, six groups of prolateral setae are here identified on the paturon (pls. 12A, 13, 14): **proventral distal (*pvd*) setae** (*gefiederte Wangenborstenreihe* of Birula, 1913), **proventral subdistal (*pvsd*) setae**, **prodorsal distal (*pdd*) setae**, **prodorsal proximal (*pdp*) setae** (*Langsreihe* of Birula, 1913), **promedial (*pm*) setal field** (*Querreihe von Borsten* of Birula, 1913; *Mittelfeld der Innerseite der Mandibeln* of Birula, 1929a), and **proventral (*pv*) setae**. These are discussed below based on “typical,” unmodified patterns. Distinct modifications of individual setae in males are mentioned, but a more detailed discussion is presented in the section on Male Flagellum and Flagellar Complex.

The proventral distal (*pvd*) setae comprise one to three regular to slightly irregular rows of straight to curved setae along the ventral prolateral margin of the fixed finger, from its base to the asetose area at its apex (Hewitt, 1919b; Birula, 1913). These setae are plumose although, in some families, the plumosity is absent or greatly reduced in all (e.g., male Hexisopodidae, pl. 129A, C, E, F) or most setae (e.g., male Rhagodidae, pl. 56C, E). The *pvd* setae are often more plumose and densely spaced proximally in the *pvd* row near the interdigital articulation, especially in females. The opposite is true for some males; the more distal *pvd* setae are increasingly modified, and often longer in some male Eremobatidae (pl. 38A, B, D), *Ceroma* (pl. 32A), and *Karschia* (pls. 30A, 31A). The proventral subdistal (*pvsd*) setae comprise acuminate setae, which are never plumose. Basal *pvsd* setae are straight, rigid, and arranged in a short, regularly spaced comblike row (Hewitt, 1919b), referred to here as the **proventral subdistal (*pvsd*) setal comb**. The *pvd* and *pvsd* setae are thus arranged in two approximately parallel series. The prodorsal distal (*pdd*) series comprises a row of approximately six to eight setae arranged in a single, often well-spaced row directly ventral to the asetose area of the fixed finger (e.g., pls. 12A, 13). The apical *pdd* and *pvd* setae are hypothesized to be primarily involved in the development of the flagellum and flagellar complex. The apicalmost seta on the fixed finger of females and immatures is typically plumose and, based on its position, identifiable as the apicalmost seta of the *pvd* series. Directly dorsal and slightly proximal to this seta is an elongated, nonplumose and slightly recurved seta identifiable as the apicalmost seta of the *pdd* series (pls. 12A, 47A). These setae or their homologs are hypothesized to give rise to the male flagellum and referred to here as the **ventral flagellar seta (*vfs*)** and the **dorsal flagellar seta (*dfs*)**, respectively (see section on Male Flagellum and Flagellar Complex). The **flagellar complex subspiniform to spiniform (*fcs*) setae** of Ceromidae (pls. 32 B, 33C), Galeodidae (pls. 4C, 30G, H, 31 E, F), Gylippinae (pls. 32H, 33I) and Karschiidae (pls. 30A–D, 31A, B) may also have originated from *pdd* setae, whereas the setiform flagellar complex of Eremobatidae (pls. 37–39), Lipophaginae (pl. 36A–F) and Melanoblossiinae (pl. 36G–I) may have developed from either or both the *pdd* and *pvd* series.

The prodorsal proximal (*pdp*) setae are situated in a row that extends longitudinally along the prodorsal surface of the chelicera, dorsal to the stridulatory plate (pls. 8–10, 12A). This row comprises two to approximately 10, relatively regularly spaced setae, sometimes with elevated sockets (pl. 8D). The *pdp* setae are always acuminate, but differ among taxa in their extent of differentiation, being weakly differentiated from the surrounding setae in *Dinorhax* and Solpugidae, pronounced and robust in Eremobatidae (pls. 12A, 72), Gylippinae (pls. 8D, 85A, C, E), and some Karschiidae (pls. 50, 51), exceptionally well developed in Rhagodidae (pl. 10), and long and slender in Ceromidae (fig. 11A, B, pl. 91A, C, E, D). The *pdp* setae are strongly prodistally directed, creating a latticelike pattern with theirserial homologs on the opposite chelicera in dorsal view (fig. 11B, D). Weaker setae may be interspersed among the *pdp* setae and a second, weaker row of setae, diverging from the prominent *pdp* setae and structurally intermediate between the *pm* and *pdp* setae (e.g., pls. 10, 58B, 72A, 73A), referred to as the **secondary prodorsal proximal *(secondary pdp)* setae**, may also be present. Birula (1913: 331) reported the *pdp* setae to be more strongly developed in male than female Gylippinae, but this was not confirmed in the present study.

The promedial (*pm*) setal field comprises a field of stridulatory setae, or homologs thereof, situated between the setal comb and the stridulatory plate (fig. 9, pls. 10, 11), and interspersed with weaker, apparently unmodified setae (see section on Stridulatory Apparatus). A dense cluster of short, fine, setiform setae lining the proximodorsal margin of the stridulatory plate is also clearly visible in dorsal view (fig. 11D). Based on structure and position, these setae are most similar to the finer setae in the *pm* setal field and are referred to here as the **promedial proximal setal cluster (*pmpc*)** (pls. 12A, 14B).

The proventral (*pv*) setae comprises a narrow, longitudinal field of setae between the ventral margin of the stridulatory plate and the ventral margin of the chelicera (pls. 12, 14A).

Movable Finger Prolateral Surface: The prolateral setae of the movable finger are situated on a narrow strip that recesses into the asetose area of the finger (figs. 12, 13, pls. 12A, 13A, 15). As with the setae on the prolateral surface of the paturon, the **movable finger prolateral setae** may be divided into different longitudinal series (rows). These setal series are named in accordance with their position (dorsal, medial, or ventral), predominant direction at origin (dorsally, ventrally, or distally directed), and setal morphology (plumose or acuminate) (fig. 13), although the ease with which series can be distinguished from one another varies among taxa (pl. 15). The dorsal setae of the movable finger, referred to here as the **movable finger prodorsal (*mpd*) setae**, are often plumose and directed dorsally to slightly dorsodistally. The putative apicalmost *mpd* seta is straight, distally directed, and resembles the apicalmost seta of the fixed finger *pdd* series (i.e., the dorsal flagellar seta, or *dfs*) in being distinctly longer than the other movable finger prolateral setae (fig. 13A, B, arrow). This seta was not observed to be plumose in the present study. The ventral setae, referred to here as **movable finger proventral (*mpv*) setae**, usually directed ventrodistally, may be straight, gently, or markedly curved distally, and were not observed to be plumose either. The more distally situated *mpv* setae are more strongly curved. A narrow field of setae, referred to here as the **movable finger promedial (*mpm*) setae**, is situated between the *mpd* row lining the dorsal margin of the setose area and the *mpv* row, lining this area ventrally. Although often curved dorsally, these setae are typically directed distally or ventrodistally at their origins. The *mpv* setae situated toward the base of the finger are often distinctly less robust than the *mpm* setae.

The prolateral setae on the movable finger of males are generally less modified than those on the fixed finger. However, in some taxa, the *mpv* setae of males become more robust and thickened toward the apex of the movable finger (fig. 13, pls. 110A, 111A, 118A, C, G), as on the fixed finger, where the setae become increasingly modified toward the apex (pl. 27). Prolateral setae on the movable finger do not appear to have been used in solifuge systematics at any level, but this character system merits further exploration, as various patterns are evident. Examples include the thin, filiform, dorsally curved tips of the distal setae of *Bdellophaga* Wharton, 1981 (pl. 87G); the slightly curved, elongated, thickened distal setae of *Eusimonia* (pl. 53A, C, E, I); two robust, ventrodistally directed subdistal *mpv* setae in male *Trichotoma michaelseni* (pl. 87C); and straight, ventrally directed *mpv* setae, curved only near the tips in all Galeodidae examined (pl. 62A, E, G, I).

Movable Finger Fondal Setae: In addition to the setae on the pro- and retrolateral surfaces of the chelicera, a short series of plumose setae projects onto the fond, where the fixed and movable fingers articulate (pls. 2B, 12A, 13A). These setae, described here for the first time, were observed in all taxa examined and are referred to as the movable finger fondal (*mff*) setae. Fondal setae arise on the proximal margin of the movable finger, with more setae situated toward the prolateral surface than the retrolateral surface. Fondal setae vary in number, plumosity, and robustness, and may therefore be of systematic importance.

Paturon Dorsal and Retrolateral Surfaces: Setae on the retrolateral surface of the paturon (**retrolateral setae**) are distinct from those on the prolateral surface, although division between series (rows) of setae is less obvious (fig. 14, pls. 12B, 16). Dorsal setae, even those originating slightly on the prolateral surface of the chelicera (pl. 17), show greatest structural similarity with setae situated on the retrolateral surface, with which they are therefore grouped here. A great diversity in form has been documented among these setae (Roewer, 1934: 120, fig. 101e), but understanding of their morphology or function is far from complete. Although relatively homogeneous in females, retrolateral setae are typically more diverse and robust in males (e.g., Roewer, 1934: 122; Lawrence, 1961: 156, fig. 1b; Martins et al., 2004; Peretti and Willemart, 2007; Hrušková-Martišová et al., 2010a), especially along the dorsodistal surface of the chelicera (cf. males in pl. 16A, C with females in pl. 16B, D). Based on

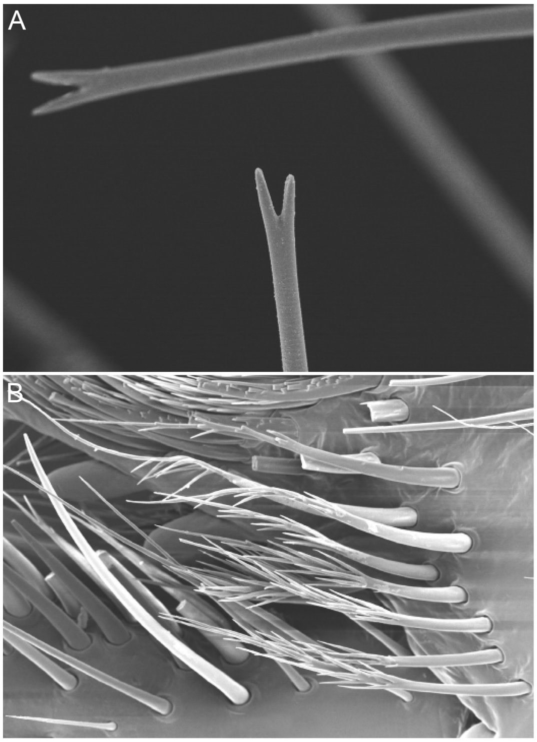

FIG. 10. Lipophaginae Wharton, 1981, *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601), chelicerae, retrolateral surface, bifid setae (**A**). Melanoblossiinae Roewer, 1933, *Melanoblossia* sp. ♂ (NMNW 13396), prolateral surface, plumose setae (**B**).

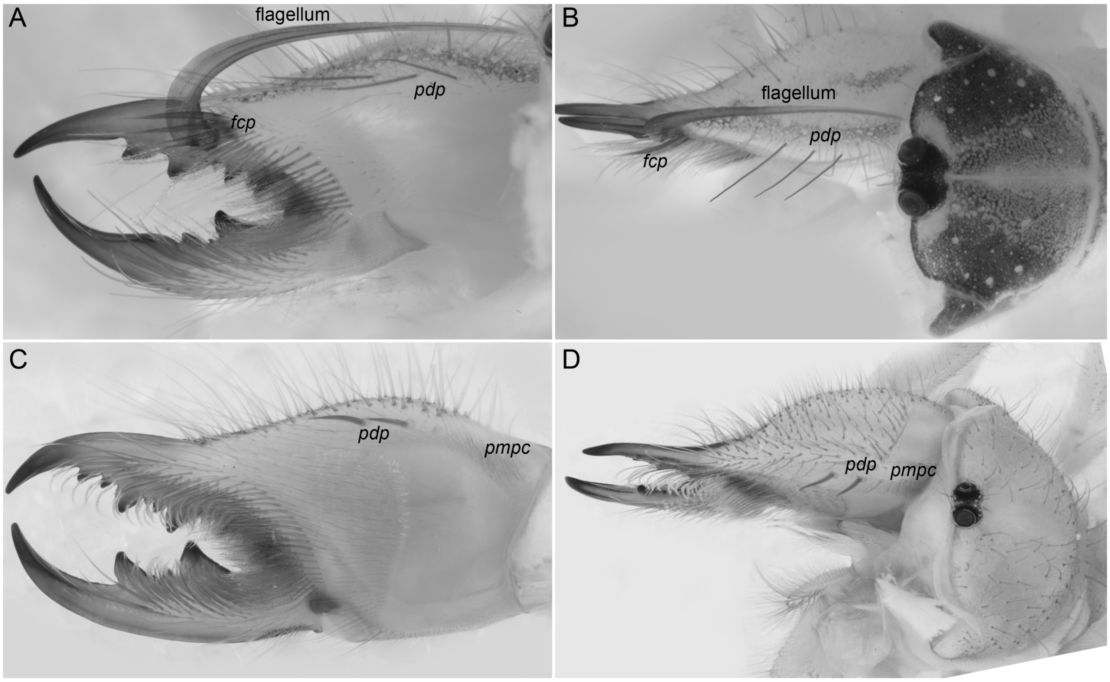

FIG. 11. Ceromidae Roewer, 1933 (**A, B**) and Eremobatidae Kraepelin, 1899 (**C, D**), chelicera and propeltidium, prolateral (**A, C**) and prodorsal (**B, D**) views, illustrating prodorsal setae. **A, B.** *Ceroma inerme* Purcell, 1899, ♂ (AMNH [LP 9864]). **C, D.** *Eremobates inkopaensis* Brookhart and Cushing, 2005, paratype ♀ (DMNS ZA.17310). Abbreviations: ***fcp*****,** flagellar complex plumose setae; ***pdp*****,** prodorsal proximal setae (enhanced); ***pmpc*****,** promedial proximal setal cluster.

similarities in shape, robustness, and directionality, the retrolateral setae may be divided into the **retrolateral manus (*rlm*) setae** and the **retrolateral finger (*rlf*) setae**.

The *rlm* setae are largely uniform in females but, in males, comprise different types of setae, usually including robust, spiniform setae (Kraepelin, 1908a) projecting almost perpendicular to the cheliceral surface. The *rlm* setae become increasingly robust and sclerotized from proximoventral to dorsodistal. Distinct differentiation of single *rlm* setae is observed only in male Gylippinae in the form of the **retrolateral manus spiniform (*rlms*) seta**, a very robust seta, the *Mandibulardorn,* which Birula (1913) considered part of the male flagellar complex (pls. 85B, 86B). Another pattern often observed in males is that in which the dorsal setae, particularly those situated slightly prolaterally, are arranged in a row along the prodorsal edge of the chelicera, curving proximoventrally near the proximal border of the chelicera (pl. 17).

The *rlf* setae are more homogeneous and characteristic in shape, position, and directionality in both sexes and all life stages of Solifugae than the *rlm* setae, and comprise several long, thin, distally directed setae, typically extending beyond the tips of the fingers (fig. 14, pl. 16). As with setae on the prolateral surface of the fingers, the *rlf* setae are arranged in three or four series (rows) along the margins of the asetose areas, with setae regularly spaced within them. Setae in the row closest to the teeth, i.e., along the asetose area of the gnathal edge, are more closely spaced, shorter, and less robust than those situated more proximally. One to three dorsal *rlf* setae are distinctly differentiated in male *Blossia* Simon, 1880 (Daesiidae), with or without spicules (fig. 14, pls. 144, 145; Lawrence, 1972, 116, fig. 6b, c), and commonly referred to as "principal setae." Lawrence (1963) cited the presence of "principal setae" as a diagnostic character by means of which *Blossia* may be distinguished from *Biton*. Lawrence's (1963) character may be redescribed as different states of the *rlf* setae: whereas the *rlf* setae of *Biton* are unmodified, *Blossia* possesses one to three modified (more robust, often spiculate) dorsal *rlf* setae. These setae were also described in other taxa, e.g., as two distinctly elongated setae in Galeodidae (pl. 16A, arrows; Lawrence, 1954: 118), but their homology with the modified *rlf* setae of *Blossia* was previously unrecognized. These dorsally situated *rlf* setae, with varying levels of modification among different taxa, are referred to here as **principal retrolateral finger (*principal rlf*) setae** (see appendix 1 for other historical uses of *principal setae*).

Movable Finger Retrolateral Surface: The **retrolateral proximal setal cluster (*rlpc*)** is a clump of setae, first identified by Muma (1985) and termed the ectal cheliceral cluster setae, or ECCS, situated proximal to the asetose area at the base of the movable finger (fig. 15, pls. 18, 19). An *rlpc* typically comprises a dorsal, weakly plumose to striated seta, and a ventral longitudinal cluster of acuminate setae, but with various apparently taxon-specific modifications. Few studies have illustrated the *rlpc* (Brookhart and Muma, 1987; Muma, 1985, 1989; Vázquez, 1991; Vázquez and Gavico-Rojas, 2000). Brookhart and Cushing (2004) mentioned investigating its potential taxonomic utility, but considered the *rlpc* uninformative for the taxonomy of the *scaber* group of *Eremobates*. The present study identified some family-level variation in setal morphology and position relative to the proximal end of the movable finger granulation (retrolateral longitudinal carina), and marked interfamilial variation in the shape of the setose area on which the *rlpc* is situated (pls. 18, 19). Examples of the shape of the setose area range from a division into two areas—a medial triangular area in addition to a narrow proximoventral area (Eremobatidae, Galeodidae, Rhagodidae; pl. 18A–F)—to fusion of the medial and proximoventral areas to form a continuous setose region proximally on the movable finger, either retaining indications of the medial asetose division (e.g., Ceromidae, Daesiidae, Gylippinae, Solpugidae; pls. 18G, H, K, L, 19A, B, E, F) or lacking any indication of the medial area (e.g., Ammotrechidae, Lipophaginae, Mummuciidae, Namibesiinae; pls. 18I, J, 19C, D, I–L). Muma (1985) identified up to four types of setae in the *rlpc* of Eremobatidae but suggested that a survey may identify more. The significance of the *rlpc* for solifuge systematics merits detailed examination and will probably provide informative characters above the species level.

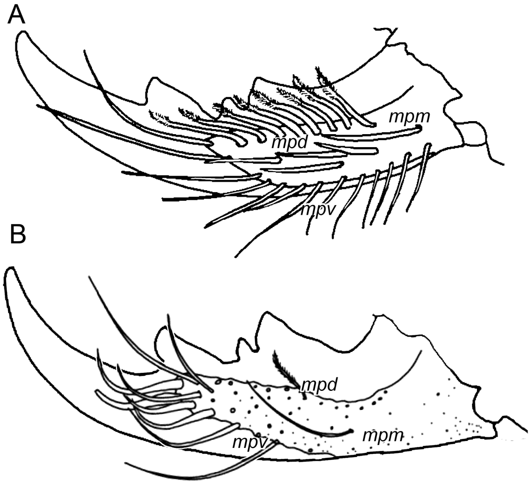

FIG. 12. Daesiidae Kraepelin, 1899 (**A**) and Solpugidae Leach, 1815 (**B**), cheliceral movable fingers, prolateral views, illustrating setae. **A.** *Blossia spinicornis* Lawrence, 1928, ♂ (NMNW), Namibia: Windhoek. **B.** *Solpugyla* sp., ♂ (AMNH [LP 10764]). Circles represent setal sockets. Abbreviations: ***mpd*,** movable finger, prodorsal setae; ***mpm*,** movable finger, promedial setae; ***mpv*,** movable finger, proventral setae.

Functional Morphology: Sexual dimorphism in the cheliceral setae is extensive but mostly unexplored. The setae of solifuges are in general more strongly developed in males than females, except for most prolateral setae, for which the opposite is true (Hewitt, 1919b: 10). Although the arrangement of prolateral setae is

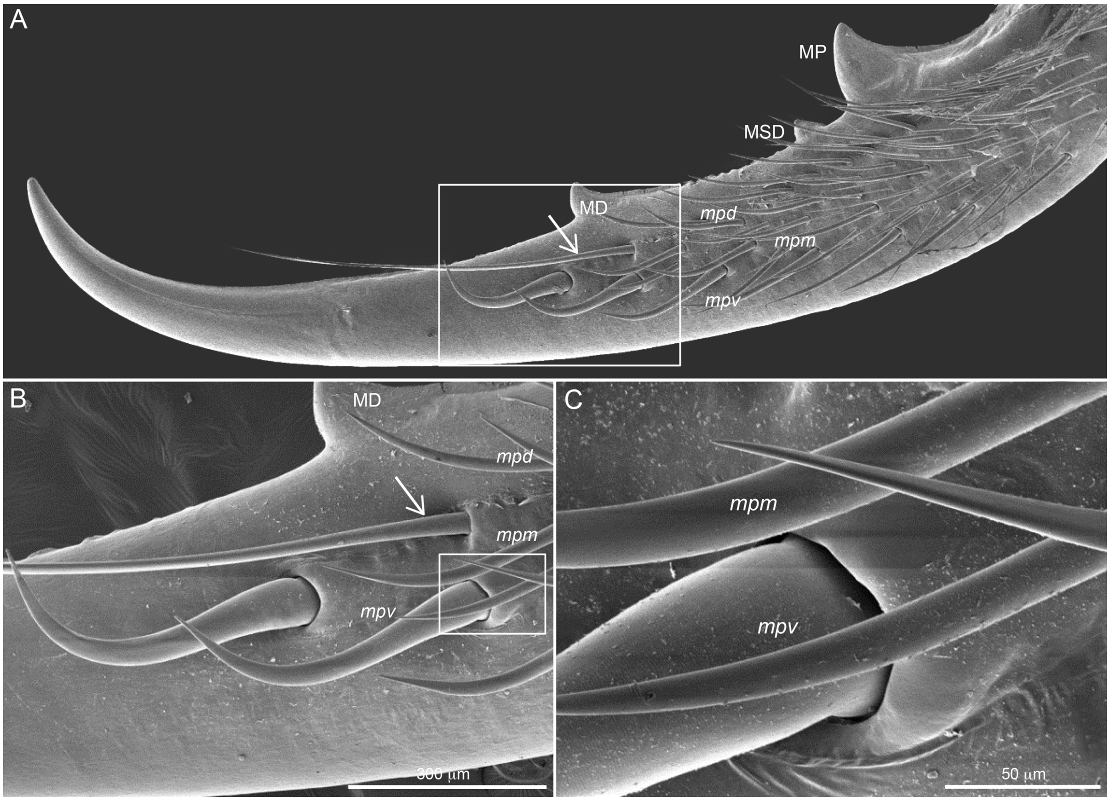

FIG. 13. Solpugidae Leach, 1815, *Solpugiba lineata* (C.L. Koch, 1842), ♂ (NMNW 13814), cheliceral movable finger, prolateral view, illustrating dorsodistally directed prodorsal (***mpd***) setae, distally directed promedian (***mpm***) setae, and ventrodistally directed proventral (***mpv***) setae (**A**); closeup of distal setal area illustrating long apical *mpd* seta (arrow) and modified distal *mpv* setae (**B**); and closeup of socket of modified subapical *mpv* seta with distally directed insertion (**C**). Additional abbreviations: **MD,** movable finger, distal tooth; **MP,** movable finger, proximal tooth; **MSD,** movable finger, subdistal tooth.

similar in both sexes, the individual setae are more or less differentiated. The prolateral setae of males are differentiated only on the distal or dorsodistal parts of the chelicera, and include the flagellum, an example of extreme setal modification in solifuges. The *pvd* setae are more numerous and strongly plumose in females than males, as exemplified by Hexisopodidae, in which the plumose setae were well developed in the females and absent in the males of all species examined. Plumose setae are probably associated with feeding, which would explain their increased plumosity and greater density in females, which appear to eat more readily than males (e.g., Wharton, 1987). With few exceptions (cf. male in pl. 50A, with female in pl. 50C), the setal comb of the *pvsd* series was not found to be sexually dimorphic. The stridulatory setae, probably serving a defensive function (see section on Stridulatory Apparatus), are also similar in both sexes.

Some of the most extensive and even less studied sexual dimorphism concerns the setae situated retro- to prodorsally on the fixed (dorsal) finger (pl. 16). The precise functions of the modified dorsal setae of male solifuges remain unknown, but they presumably play a role in mating (table 2). Based on observations that these setae are situated on the part of the chelicera that comes into close contact with the female's genital area during mating (e.g., Peretti and Willemart, 2007; Hrušková-Martišová et al., 2010a), these setae may collect chemo- or mechanoreceptory cues from the female. Another possible function of the dorsal setae, first suggested by Pocock (1895), may be to protect the flagellum. The arrangement of the dorsal setae indeed appears to be optimal for protecting some types of flagella such as those of Ceromidae (pl. 91E, F), *Hemiblossia* (Daesiidae, pl. 139G, H), and Galeodidae (pl. 59A–D). Even if these setae perform a protective function in some taxa, however, that is unlikely to be their only function.

In conclusion, male solifuges exhibit greater differentiation among the setae of the dorsal and retrolateral cheliceral surfaces, and the apices of the prolateral surfaces of the cheliceral fingers, but less differentiation (or a similar level of differentiation to the female) among the setae on the prolateral cheliceral surfaces. The opposite is true of females (Hewitt, 1919b). This structural difference implies a functional division between the prolateral surfaces of the chelicera used primarily for feeding (and secondarily, in at least some taxa, for defense), and the dorsal and retrolateral surfaces of the chelicera and prolateral apices of the fingers, which are modified for mating. Finally, immatures generally exhibit fewer setae, arranged in a more orderly pattern, than adults (Hewitt, 1919b: 10).

Taxonomic Diversity of Cheliceral Shapes, Processes, and Chaetotaxy

Ammotrechidae: Ammotrechid male chelicerae range from slender and relatively unmodified (pl. 146) to highly modified, with some relatively robust. Most ammotrechid cheliceral modifications concern the mucra of the fixed and/or movable fingers, including pro- and retrolateral flanges on the fixed finger mucron, especially prominent in *Pseudocleobis* Pocock, 1900 (e.g., pl. 146A, B; Maury, 1976: 96, figs. 13, 14, 18, 19, 21, 22; 1980b: 42, figs. 1–4). A medial notch is present in some species (fig. 7D). Dorsal hornlike processes and cheliceral spines are absent. A pronounced angular dorsal margin on the fixed finger of females, referred to here as a **dorsal crest** (Muma, 1951: 126, figs. 273–4; Maury, 1982: 141, figs. 36, 44), similar to the dorsal crest of female Mummuciidae (pl. 151E), is common in Ammotrechidae. The crest of females is unusual among Solifugae in which females are usually more conserved in cheliceral shape than males.

Ceromidae: In the chelicerae of typical ceromid males, except for *Ceroma inerme* Purcell, 1899, the fixed finger is shorter than the movable finger and a prolateral flange is situated parallel to the **movable finger medial (MM) tooth** (pls. 91–95; also see section on Dentition). No other processes or flanges are present. The chelicerae of *Toreus* are highly modified and appear to be unlike other ceromids. Purcell's (1899: 400) description of the dorsal finger of *Toreus* as "divided into two portions" is reminiscent of *Trichotoma michaelseni*, which possesses a hornlike process fused dorsally to the fixed finger (pls. 87A, C, 88C). However, the phylogenetic placement and even the sex of the holotype of *Toreus* are uncertain (Lawrence, 1962b; Muma, 1976; Wharton, 1981; also see section on Taxonomic Overview). Modified setae that form part of the flagellar complex are discussed in the section on Taxonomic Diversity of the Flagellar Complex.

Daesiidae: Daesiid male chelicerae display diverse shapes, from relatively unmodified, to bizarre modifications such as the extremely elongated fixed finger of *Ceratobiton styloceros* (Kraepelin, 1899) (pl. 137D) and the chelicera apparently adapted for burrowing in *Gnosippus klunzingeri* Karsch 1880 (pls. 136C, D, 137A, B). In the latter, the *rlf* setae are short, stout, and spiniform, creating a rostrumlike distal finger apparatus. Various daesiids also exhibit cheliceral processes and projections such as the pronounced dorsal hornlike process (**spine**) of *Ammotrechelis goetschi* (pls. 132E, F, 134A) or the short, distally projecting dorsal spine of various shapes in *Biton* (*B.*) *gariesensis* (Lawrence, 1931) (Lawrence, 1931: 134, fig. 3A, B) and *Blossia echinata* Purcell, 1903 (see Purcell, 1903b: pl.1, fig. 9); a rugged retroventral lamina at the apex of the fixed finger, e.g., in *Biton* (*B.*) *cataractus*

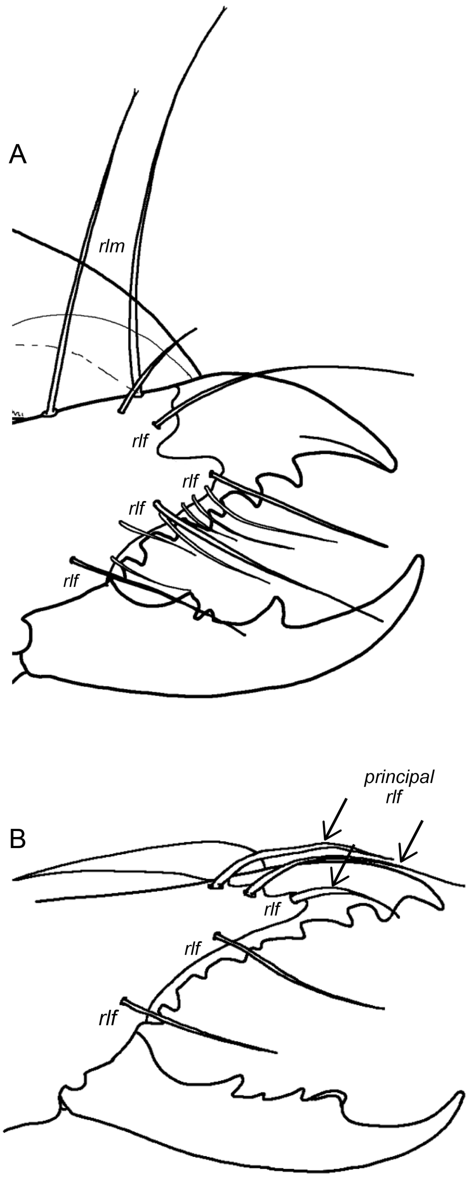

FIG. 14. Daesiidae Kraepelin, 1899, chelicerae, retrolateral views, illustrating positions of some *rlf* setae. **A.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]), illustrating arrangement of *rlf* setae in rows, and dorsally situated, bifid *rlm* setae. **B.** *Blossia* cf. *rooica*, ♂ (NMNW), Namibia: Gondwana Cañon Park, illustrating unmodified *rlf* and modified *principal rlf* setae. Abbreviations: ***rlf***, retrolateral finger setae; ***rlm***, retrolateral manus setae.

Lawrence, 1968 (Lawrence, 1968: 72, fig. 4c) and *Blossia hessei* Lawrence, 1929 (Lawrence, 1929: 174, fig. 16); a marked concavity in the ventral tip of the fixed finger apparently to accommodate the distal tooth (DT) of the movable finger, e.g., in *Biton* (*B*). *ehrenbergi* Karsch, 1880 (Roewer 1934: 389, fig. 275b1, b2; El-Hennawy, 1998); and a large, concave medial tooth on the movable finger (MM) to accommodate the fixed finger medial (FM) tooth, e.g., in *Biton* (*B.*) *truncatidens* Lawrence, 1954 (pl. 137C). The apices of the fixed and movable fingers of male *Namibesia pallida* are twisted and markedly concave in ventral and dorsal views, respectively. A broad flange, which appears to be a prolaterally displaced gnathal edge, situated prodistally on the fixed finger, and approximately perpendicular to the prolateral surface of the finger, forms a ventral concavity (pls. 132A, 133A). Flanges and toothlike structures on the gnathal edges of the fingers of *Blossia* are described elsewhere (see section on Dentition). The fixed finger is straight and narrow, resembling the mostly styletlike fixed fingers of Eremobatidae, in several species of *Biton*, e.g., *Biton* (*B.*) *kraekolbei* Wharton, 1981 (Wharton, 1981: 15, fig. 8; Roewer, 1934: 389, figs. 275 $a_{1,}$ $f_{1,}$ g, h_1). As in Eremobatidae, this shape is accompanied by a reduction in the dentition, especially distally, on the fixed finger. A relatively short finger with a straight dorsal margin is common in southern African *Biton* and also occurs in *Eberlanzia* Roewer, 1941 (pl. 143). The prodorsal proximal series of setae varies from weakly to well differentiated.

Among the setae of the retrolateral finger (*rlf*) series, one or two of the dorsodistal setae, situated slightly below the upper margin of the chelicera on the retrolateral surface, are thicker and less filiform, and differ in the presence/absence and extent of spicules. These modified setae, common in *Blossia*, are termed the *principal rlf* setae (fig. 14B, pls. 144, 145). The number of *principal rlf* setae, and the extent and position of spicules on these setae are important in *Blossia* systematics (e.g., Hewitt, 1919b: 58, fig. 10; Lawrence, 1935, and figures therein).

Dinorhaxinae: The cheliceral shape of *Dinorhax*, with its low aspect ratio (cheliceral length/cheliceral height) resembles the chelicera of Rhagodidae, in which *Dinorhax* was originally placed by Simon (1879), and Hexisopodidae. The cheliceral similarity, together with the short, robust legs, are consistent with a fossorial habitus, but no life history data are available for *Dinorhax* to confirm that. The dorsal mucron is angular, pointing ventrodistally (pls. 56A, B, 57A, B). The movable finger possesses a blunt, angular, and longitudinal retrolateral surface (movable finger retrolateral carina, MRLC) into which the rounded proximal margin of the fixed finger closes (pls. 56B, 57B), similar to the MRLC of Rhagodidae (pl. 56D, F, H) and Hexisopodidae (pl. 126F–H).

Eremobatidae: Eremobatid males display some of the most highly modified chelicerae among Solifugae, including a cheliceral manus that narrows proximally, becoming wider distally in most species. A typical eremobatid male fixed finger possesses a vertical fond with unusually well-developed fondal teeth, distal to which the finger narrows abruptly into a toothless or nearly toothless, narrow stylet (males in pls. 65, 67, 68). A characteristic of Eremobatidae is the presence of a notch proximal to the FP tooth (fig. 7A, B), termed the **fondal notch (FN)** by Muma (1951) and used extensively in eremobatid taxonomy (e.g., Muma, 1951; Brookhart and Cushing, 2002). The notch is usually well developed, especially in species with a narrow fixed finger (pls. 65–68). Deviations from this distinct styletlike shape are usually associated with a shorter and/or less vertical fond and a weak to absent fondal notch as in, e.g., *Eremochelis* (pl. 76) and *Hemerotrecha* (pls. 79, 82).

The styletlike fixed finger of eremobatid males varies from straight to curved, the latter resulting in a slight upturn or **fixed finger crimp**, e.g., in *Eremobates corpink* Brookhart and Cushing, 2004 (pl. 67A, B). Brookhart and Cushing (2004) noted a positive correlation between the degree of curvature and the depth of the fondal notch in the *scaber* group of *Eremobates*. A **retrodorsal process (RDP)** (ectodorsal process of Muma, 1951) is present at the base of the fixed finger in the *palpisetulosus* group of *Eremobates*, and varies from a low ridge, barely distinguishable from the dorsal margin of the finger, e.g., in *Eremobates palpisetulosus* Fichter, 1940 (pls. 68D, 69D), to a tall, flangelike process, e.g., in *Eremobates tuberculatus* (Kraepelin, 1899) (pls. 68J, 69F).

The **flagellar groove** is a longitudinal prolateral groove that accommodates the cryptic eremobatid flagellum (pls. 38, 39A–E, H). Variation in length (extending along the entire length of the finger or restricted to the distal part thereof) and shape (distinct or indistinct creaselike or

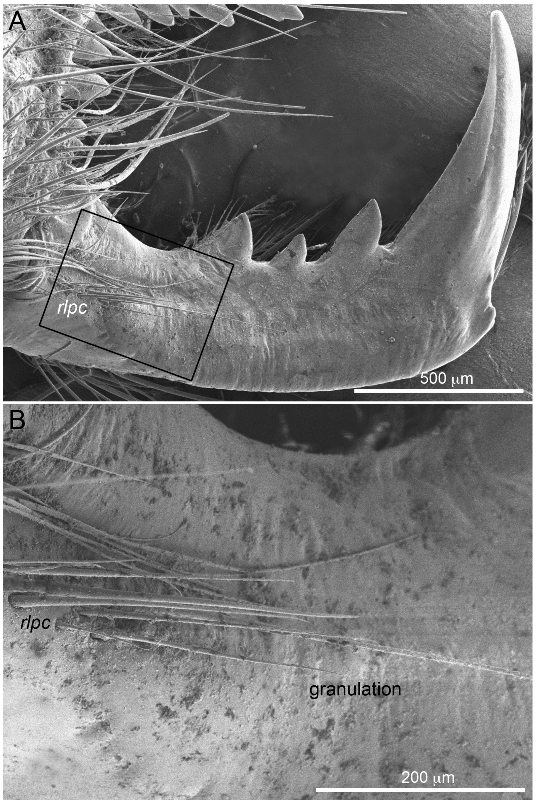

FIG. 15. Lipophaginae Wharton, 1981, *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601), cheliceral movable finger, retrolateral view, illustrating retrolateral proximal setal cluster (***rlpc***) and position of asetose area. Rectangle in **A** indicates area in **B**.

cuplike concavity) is significant for the taxonomy of genera and species groups (Muma, 1951: 39; Brookhart and Brookhart, 2006), e.g., widening of the base of the flagellar groove into a cuplike, enlarged proximal concavity (pl. 39B) in the *pallipes* group of *Eremobates* (vide Muma, 1951). Brookhart and Muma (1981: 287, 288) noted "subtle" differences among populations in the "length, width, and pitch" of the basal flange of the groove, and found these useful for separating species in combination with other characters. An oval, proventral to retroventral, well-defined cuplike concavity on the asetose area of the fixed finger of male Eremobatidae, e.g., *Eremocosta* (pl. 73B), is referred to here as a **ventrodistal concavity** (pl. 37C).

Prodorsal proximal (*pdp*) setae are often pronounced in Eremobatidae, sometimes with enlarged sockets, and an additional, more weakly developed row of *secondary pdp* setae is often situated ventral to the primary row (pl. 73A). In addition to the "typical" eremobatid cheliceral shape, enlarged *pdp* sockets are shared by some eremobatids and the gylippines examined (pls. 12A, 85A, C, E). Eremobatid stridulatory setae are unique in being inserted on swollen, elevated sockets, unlike the modified stridulatory setae of other taxa in which the setal bases are swollen (fig. 9, pl. 11E).

Galeodidae: The shape of the galeodid male chelicera is relatively conserved, with modifications restricted to the mucra (males in pls. 59, 62). A small, prolateral circular blemish, usually on a slight, toothlike elevation, is situated near the base of the mucron on the prolateral surface of the fixed finger (pl. 60A). It was observed in all specimens examined and is referred to here as the mucron organ (mo). A similar structure is present in Ammotrechidae, Solpugidae (fig. 24B, pl. 27E), and Mummuciidae (R. Botero-Trujillo, personal commun.). No distinct processes or flanges are present on the chelicera of Galeodidae. At rest, the flagellum is surrounded by numerous erect spiniform setae on the fixed finger (Pocock, 1895) (pl. 30G). These are similar to the apically truncate cylindrical setae, often found on the pedipalps, but longer, more robust, and with a swollen tip. At least three types of stridulatory setae have been identified in galeodids (fig. 9A–C, pl. 11G–I). Modified setae that form part of the flagellar complex are discussed in the section on Taxonomic Diversity of the Flagellar Complex.

Gylippinae: The chelicera of a typical male gylippine (pls. 85A, B, 86A, B) resembles that of a male eremobatid with a vertical fond, reduced dentition on a styletlike fixed finger, and a manus that is narrowed proximally, becoming wider distally. The fixed finger narrows abruptly and remains styletlike until the apex. The teeth of the median series are highly reduced, at most vestigial. Additional structures on the prolateral surface of the male chelicera, the dental papillae, occur on the sclerotized area adjacent to the gnathal edge of the fixed finger, at the base of the teeth in *Gylippus* (*Anoplogylippus*) species. Unfortunately no species of this subgenus were available for study. The presence and number of dental papillae varies interspecifically (Birula, 1938: 93, 96, figs. 64, 61). Prominent swollen sockets of the prodorsal proximal (*pdp*) setae present in specimens examined (pls. 8D, 85A, C, E) are similar to those of some eremobatids.

In addition to a very robust *rlm* seta in males (i.e., the retrolateral manus spiniform seta, or *rlms*), a group of *rlm* setae are distinctly spiniform (pl. 85B) and regarded by various authors as unique to Gylippinae. These are referred to as *Spina accessoriae* by Roewer (1934: 308) and *Nebendornen* by Birula (1913: 332), who also referred to the spiniform setae associated with the galeodid flagellar complex (*fcs*) as *Nebendornen*. These "accessory spines" are probable homologs of the *rlm* setae, with similar examples of increased robustness observed in other families, e.g., Eremobatidae (pl. 76F), Galeodidae (pl. 62 H), and Solpugidae (pl. 121B), and are thus not unique to gylippines, but are simply regular *rlm* setae with a strongly spiniform character. Modified setae that form part of the flagellar complex are discussed in the section on Taxonomic Diversity of the Flagellar Complex.

Hexisopodidae: Hexisopodid chelicerae are compact and robust in both sexes, presumably an adaptation to the exclusively fossorial existence of these solifuges (pls. 126–130). The cheliceral fingers of hexisopodids are sexually dimorphic in shape, being more slender in males. In females, the base of the movable finger, along the granulation row, forms a blunt, angular, and longitudinal retrolateral elevation (the movable finger retrolateral carina, MRLC), which accommodates the base of the fixed finger (pl. 126F–H). A weak MRLC is present in some males. Similar, but more angular and less granular retrolateral carinae are present in *Dinorhax* (at least in males; pls. 56B, 57B) and Rhagodidae (both sexes; pl. 56D, F, H). The granular row is more densely granular below the movable finger medial (MM) tooth in females (pl. 126F). Prominent, randomly spaced granules, in addition to the regular granular row, are also more distinct in females.

The asetose area on the fixed finger of both sexes is modified to form a lobate, sclerotized area, termed the callus (fig. 6A; Lamoral, 1973; Wharton, 1981). The number of tubercles on the callus has been used in species diagnosis (e.g., Lawrence, 1949b; Lamoral, 1973). Tubercles on the callus may vary in size (Wharton, 1981: 52), perhaps due to wear. A well-developed, longitudinal flangelike carina (prolateral flange) at the apex of the fixed finger, usually terminating in a sharp point distally, occurs in some species (pl. 127B; Lawrence 1967: 14, fig. 7a–c), creating the unusual shape of the fixed finger in dorsal view (fig. 6A). This carina is not considered homologous to the prodorsal flangelike flagellar groove process (FGP), associated with the flagellar groove that accommodates the base of the **flagellar shaft** in Solpugidae (pl. 20D). Wharton (1981: 52) reported the "shape of flange either variable, or subject to considerable wear."

The propeltidium and dorsal surfaces of the chelicerae of *Chelypus hirsti* Hewitt, 1915 are randomly covered with globular setae that have not been observed in other families (seen in the irregular dorsal surface of the manus in pl. 129D, E; Lawrence, 1949b; Lamoral, 1973: 97, fig. 7c). Plumose setae appear to be absent on the chelicerae of male Hexisopodidae.

The unusual case of *Siloanea* merits discussion in the context of hexisopodid cheliceral modifications. *Siloanea* was established by Roewer (1934: 339) based on several noncheliceral characters exhibited by the holotype of *Siloanea macroceras* Roewer, 1933 (currently placed in *Chelypus*), the sex of which was uncertain. Roewer (1934) identified the holotype of *Siloanea eberlanzi* Roewer, 1941, the second species of the genus to be described, as an adult male. No flagellum is present in either specimen. However, the chelicerae of both display one or more dorsal hornlike processes on the fixed finger. Lawrence (1966: 6, fig. 3d) argued that the holotypes of *Siloanea* are merely female specimens of *Chelypus*, none of which had been described at the time, and described a specimen with cuticular hornlike processes, displaying close affinities with *Siloanea*, as the female holotype of *Chelypus coatoni* Lawrence, 1966 (currently in synonymy with *Chelypus lennoxae* Hewitt, 1912). Lamoral (1973) disagreed with Lawrence (1966), reidentified the holotype of *Chelypus coatoni* as a male, transferred this species to *Siloanea*, and revalidated the latter. Wharton (1981) agreed with Lawrence (1966), however, and synonymized *Siloanea* with *Chelypus*, proposing *Chelypus lawrencei* Wharton, 1981, as a replacement name for *Siloanea eberlanzi*, a junior secondary homonym of *Chelypus eberlanzi* Roewer, 1941. Although the strong, hornlike processes are unusual for female solifuges, the well-developed dentition (Lawrence, 1966: 6, fig. 3d), plumosity of the proventral distal (*pvd*) setae, and presence of two malleoli (e.g., Lawrence, 1966) are typical characters of female Hexisopodidae. Assuming all three holotypes are indeed female, as the absence of a flagellum suggests, these species would represent rare examples in which the female chelicera is highly modified.

Karschiidae: Male Karschiidae possess a low prolateral flange approximately parallel or distal to the medial tooth (MM) on the movable finger, creating a small troughlike concavity (“spoon-shaped excavation” sensu Lawrence, 1954: 112). This structure may serve to protect the flagellum (fig. 16). The dorsal mucron in both sexes of *Eusimonia* is sinuous and curved ventrally (pl. 53; Birula, 1938; Gromov, 2000). The fixed finger of male *Karschia* commonly exhibits a relatively straight dorsal margin, with a markedly angular ventrodistal bend in the mucron, and a tendency toward a vertical fondal area (pls. 50B, F, 52A; Birula, 1938: fig. 20, 25; Gromov, 1998: 181, fig. 1j) resembling that of male Eremobatidae. A small dorsoproximal toothlike protuberance (**dorsal cheliceral spine**) occurs in some *Karschia* males (*r* and *rh* sensu Birula, 1938) and a distally directed hornlike process occurs in males of all but one species of *Eusimonia* (e.g., *rh* sensu Birula, 1938; Muma, 1982; Gromov, 2000).

The prolateral setae of Karschiidae differ from those of other Solifugae in differentiation and position. The comb of *pvsd* setae is weakly differentiated in female *Karschia* (pl. 50C) and both sexes of *Eusimonia* (pl. 53). The comb is often situated more dorsally and arranged horizontally, rather than the typical medial position and vertical arrangement observed in most Solifugae (e.g., pls. 52B, 54A). The various apical series of setae on the fixed finger (*pvsd*, *pdd*, and *pm*) are not readily distinguished (e.g., pl. 53) and the *pvd* setae greatly reduced in males (pl. 53A, C, I). Modified setae that form part of the flagellar complex are discussed in the section on Taxonomic Diversity of the Flagellar Complex.

Lipophaginae: The mucron of the movable finger is markedly curved dorsally in male *Lipophaga* and *Trichotoma*, and angulate in *Bdellophaga* Wharton, 1981 (pls. 85G, H, 87A–D). These mucra are deeply concave dorsally, i.e., on the gnathal edge (Wharton, 1981), especially in *Trichotoma*, and this concavity is more pronounced in males than females (pl. 87). No cuticular processes are present in Lipophaginae, except for an unusual structure, hypothesized to be a dorsal hornlike process that is fused to the dorsal finger in *Trichotoma michaelseni* (see section on Taxonomic Diversity of Cheliceral Dentition).

Melanoblossiinae: The chelicerae of Melanoblossiinae are long and slender in both sexes. Males possess a prolateral concavity that accommodates the **setiform flagellar complex (*sfc*)**, referred to here as the **flagellar complex depression** (pl. 36G–I). The ventral location of the flagellar complex creates a **medioventral excrescence (MVE)** in the fixed finger that may be weak (pl. 158C) or pronounced (pls. 156B). Modified setae are absent on the melanoblossiine chelicera except for the setae comprising the setiform flagellar complex. Processes and flanges are also usually absent, except in an undescribed *Melanoblossia* species with elaborate modifications distally on the fixed finger (figs. 6B, 26A; pls. 154G, H, 157).

Mummuciidae: Mummuciid chelicerae are fairly conserved, differing little in shape between the sexes (pls. 149E–H, 151, 152). The most prominent modifications in the male chelicerae concern the flagellar groove, formed by prodorsal and prolateral flangelike carinae on the fixed finger, referred to here as the **prodorsal carina** and **proventral carina**, respectively (pls. 34G, H, 35H, I, 152B), which accommodate the flagellum (e.g., Carvalho et al., 2010: 25, figs. 13, 15, 16; Botero-Trujillo, 2014: 325, figs. 13, 15). The prodorsal carina was referred to as the “dorsal keel” by Botero-Trujillo (2014: 321, 325, fig. 16). A low but distinct and angular dorsal crest, situated approximately dorsal to the fixed finger distal (FD) and fixed finger medial (FM) teeth, and referred to as the “dorsal hump” by Iuri et al. (2014: 21) and Botero-Trujillo (2014: 321, 325, figs. 11, 17), is present on the fixed finger of females (pl. 151E). A less angular dorsal crest, situated opposite the widest part of the flagellum, which it probably serves to protect (pls. 149E–H, 151C, D, 152B, C), is also present on the fixed finger of some males.

Botero-Trujillo (personal commun.) observed a mucron organ (mo) similar to that of Galeodidae and Solpugidae, in female and immature mummuciids, but noted that these are unclear in scanning electron micrographs. Other modifications concern, at most, the shape of the mucra of the fingers, particularly the fixed finger.

Rhagodidae: Rhagodid chelicerae are robust and compact in both sexes, being slightly more slender in males (pls. 56C–H, 57C, D, 58). A blunt, angular retrolateral surface (movable finger retrolateral carina, MRLC), into which the rounded proximal margin of the fixed finger closes (pl. 56D, F, H), is observed in both sexes, and similar to that observed in *Dinorhax* (at least males; pls. 56B, 57B) and Hexisopodidae (pl. 126F–H).

Distinct macrostructures (flanges, cheliceral processes, etc.) are absent. Prodorsal proximal (*pdp*) setae are exceptionally robust and pronounced in most species, and a row of *secondary pdp* setae are present. Stridulatory setae (fig. 9D, pl. 10, 11F) are similar to the type II (*araneoides* type) setae of Galeodidae (fig. 9B, pl. 11G, H) and apparently not restricted to the field between the stridulatory plate and the *pvsd* setal comb, but extend dorsal to the stridulatory plate to form the row of *secondary pdp* setae.

Solpugidae: *Solpugema* is partly characterized by a medial notch (fig. 7C), which is not considered homologous to the fondal notch of Eremobatidae (fig. 7A, B). The medial notch may be strongly curved, e.g., in *S. derbiana* (Pocock, 1895) (pl. 108F) to sublinear, e.g., *S. brachyceras* (Lawrence, 1931) (pl. 108D). Although Roewer (1934: 466) identified the medial notch as a diagnostic character for *Solpugema*, the length of the toothless gap varies, and there is some overlap between its length in *Solpugema* and other genera. For example, the short, shallow notch of *Solpugema hamata* (Hewitt, 1914) (pl. 106J; Hewitt, 1914b: 160, fig. 22) is not significantly different from that in *Solpugista hastata* (pl. 110I; Kraepelin, 1901: 59, fig. 15) or *Solpuga chelicornis* Lichtenstein, 1796 (pl. 102B, E).

The diversity of cuticular modifications associated with the tip of the male cheliceral fixed finger of Solpugidae rivals that of all other solifuge families (pl. 20). These modifications include toothlike processes, carinae, and flanges, and the mucron may also be distinctly modified. These structures appear to be associated with insertion of the flagellar shaft into a furrow in the fixed finger, the flagellar groove, forming by distal extension of its prolateral rim, and are generically referred to here as **flagellar groove processes (FGP)**. Flagellar groove processes (FGP) may take the form of a weakly elevated carina as in *Zeria carli* (Roewer, 1933) (pl. 20B) and *Zeria venator* (Pocock, 1897) (pl. 20C); a long, smooth flangelike carina as in *Solpugiba lineata* (C.L. Koch, 1842) (pl. 111A), *Solpuga chelicornis* (pl. 20D), and *Oparba asiatica* (Turk, 1948) (pl. 27E); a short, markedly curved carina as in *Solpugema derbiana* (Pocock, 1895) (pl. 108E) and *Solpugema hamata* (pls. 20G, 106I); a jagged, toothlike carina situated dorsally as in *Solpugema intermedia* (Lawrence, 1929) (pl. 109F) and *Solpugema montana* (Lawrence, 1929) (pl. 109E); a jagged, ridgelike carina situated prodorsally as in *Solpugema brachyceras* (Lawrence, 1931) (pls. 20H, 108C); or an elongated carina situated prodorsally as in *Solpugema genucornis* (Lawrence, 1935) (pl. 20F), and *Solpugista bicolor* (Lawrence, 1953) (pl. 20E). A mucron organ (pl. 20A), often situated on a toothlike structure (e.g., fig. 24B, inset), is present even in the absence of a distinct FGP. Pocock (1897: 264) described the medially pointed toothlike process, situated prolaterally on the apex of the finger in *Solpugassa dentatidens* (Simon, 1879) and *Zeria ferox* (Pocock, 1895), as a **supernumerary tooth** and hypothesized that it functions to prevent closure of the movable (ventral) finger. The flagellar groove processes (FGP) of male Solpugidae are used extensively for species diagnosis in the family (e.g., Pocock, 1897; Lawrence, 1955). The extent of intraspecific variation in these structures has never been evaluated, however, and there is evidence that such variation exists. For example, according to Simonetta and Delle Cave (1968), prolateral “tubercles” (toothlike

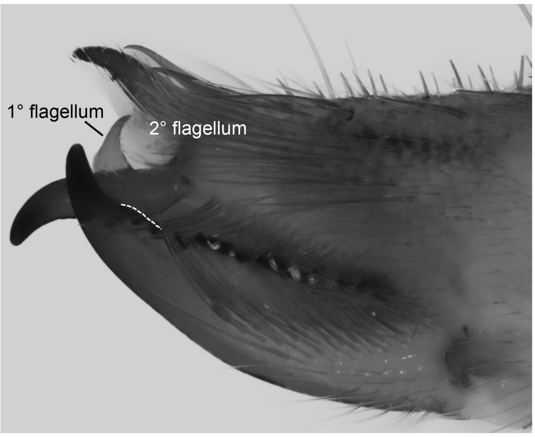

FIG. 16. Karschiidae Kraepelin, 1899, *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]), closed cheliceral fingers, prolateral view, illustrating location of flagellum in troughlike depression between prolateral flange (indicated with stippled line) and gnathal edge of movable finger. Abbreviations: **1°,** primary; **2°,** secondary.

flagellar groove processes, FGP) were present in some but not all specimens of *Zeriassa lepida* Kraepelin, 1913 (*N* = 9) examined. Such variation may, however, be an artifact of wear.

The prodorsal proximal (*pdp*) setae are weakly differentiated in Solpugidae, and the promedial (*pm*) setae are not modified into stridulatory setae.

Summary of Cheliceral Morphology

The two-segmented solifuge chelicera comprises a paturon (manus plus fixed, or dorsal, finger) that articulates with the movable (ventral) finger. The chelicerae of solifuges are unique among arachnids because they play a prominent role during mating behavior and sperm transfer, in addition to a suite of other functions such as feeding, defense, and burrowing. The diversity of functions is reflected in the richness and regional specialization of characters on the chelicera.

Little evidence of sexual dimorphism exists in characters such as granulation on the asetose areas of the fingers, and the development of stridulatory ridges and stridulatory setae. If sexual dimorphism is present, however, these characters are often more developed in females than males, suggesting nonreproductive functions such as feeding and defense.

Males have more gracile chelicerae than females, with a higher aspect ratio, likely due to reduced feeding, but differences in the shape of the male fixed finger appear more related to reproduction. Similarly, processes such as carinae, flanges, and hornlike structures are absent in females, but may be diverse in males of some families, especially Solpugidae. The mucron organ (mo) is present in both sexes of Galeodidae and Solpugidae, and at least some Ammotrechidae and Mummuciidae. It may prove to be more widely distributed on account of its cryptic disposition.

The rich chaetotaxy of solifuges is also extended to the chelicera, but the setae on the pro- and retrolateral surfaces of the chelicera differ markedly in morphology and arrangement. Sexual dimorphism in setae indicates regional specialization on the chelicera correlated with different functionality. Retrolateral setae, particularly on the manus, are more randomly distributed, whereas prolateral setae are arranged in distinct, recognizable series and setal fields. Bifid setae, common and pronounced in solifuges, appear to be absent on the prolateral surface, whereas plumose setae are restricted to it. Most modifications in male setae concern the retrolateral manus (*rlm*) setae and prolateral setae toward the apices of the fingers, especially the fixed finger. Setae in these regions of the chelicera tend to be largely homogeneous in females.

DENTITION

Historical Perspective and Background

The dentition pattern refers to the size, shape, position, and number of teeth on the cheliceral fingers of Solifugae (pls. 21, 22). A summary of the types of teeth is provided in table 6. Dufour (1861: 350) was the first to formally distinguish types of teeth. Based on a male *Oparbella aciculata* (Simon, 1879) and a female *Galeodes olivieri* Simon, 1879, both as *Galeodes dastuguei* Dufour, 1861, Dufour (1861) termed the larger teeth "canines," the smaller teeth between them, "incisors," and the two rows of basal teeth on the fixed finger, "molars." Dufour (1861) regarded 16 teeth per chelicera (6 incisors, 4 canines, and 6 molars) as typical for solifuges. Pocock (1889) referred to the large proximal tooth on the movable finger as the principal tooth.

Kraepelin (1899, 1901) proposed the first comprehensive terminology for the cheliceral dentition of Solifugae, and applied it to the diagnosis of species except those with highly modified dentition, e.g., *Ceratobiton styloceros,* placed in the genus *Gnosippus* at the time. Kraepelin (1901: 101) referred to the two large distal teeth and any smaller teeth between them, as *Vorderzähne* ("front teeth"); the large, proximal tooth, as *Hauptzahn* ("main" or "principal tooth"); the smaller teeth between them, as *Zwissenzähne* ("intermediate teeth"); and the two diverging rows of small teeth at the base of the fixed finger, as *Wangenzähne* ("cheek teeth"). Kraepelin (1901: 99, 1908b: 277) referred interchangeably to two principal teeth (similar terminology was applied by Pocock, 1900a) or to a principal and an anterior tooth on the movable finger. Kraepelin (1901) supplemented terminology with a numbering system to specify the relative positions of teeth within the series, permitting the dentition to be more precisely defined, e.g., "*4. Hauptzahn*" indicated that the primary tooth is the fourth from the tip of the fixed (dorsal) finger.

Except for the numbering, Kraepelin's (1899, 1901) terminology continued to be followed exactly (e.g., Roewer, 1934: 53; Kraus, 1956; Panouse, 1956, 1960a, 1960b; Simonetta and Delle Cave, 1968; Armas 1994) or with some modifications. Early South American workers used "basal teeth" for cheek teeth (Mello-Leitão, 1938; Maury, 1970, 1984; Armas, 2002) whereas Muma (1951: 38, fig. 5), followed by other North American workers, used "fondal teeth" for cheek teeth and "medial tooth" for the middle primary tooth of the fixed finger. Nonetheless, a standard reference to the terminology of the cheliceral dentition remained elusive. Muma's (1951) modifications to Kraepelin's (1899, 1901) terminology are followed mainly by New World workers (e.g., Brookhart, 1965), often with further minor changes, e.g., Brookhart and Cushing (2004, 2008) and Catenazzi et al. (2009) used "primary tooth" instead of "principal tooth." Rocha and Carvalho (2006) followed Muma (1951) in the use of "fondal," but followed Kraepelin (1899, 1901) and Maury (e.g., 1970, 1982) in the use of "anterior teeth." Carvalho et al. (2010) followed Rocha and Carvalho (2006), the only recent studies that referred to the small (submedial) tooth on the fixed finger as a "second principal tooth." Botero-Trujillo (2014) recently provided a more comprehensive terminology, e.g., Fa_1 for the distalmost primary tooth, but did not distinguish between primary and **secondary teeth** among the three distalmost teeth on the fixed (dorsal) finger. Botero-Trujillo's (2014) subscripts are, however, useful to distinguish among individual secondary teeth within a category, e.g., two secondary teeth between the proximal and distal **primary teeth** on the movable finger.

Although Kraepelin's (1899, 1901) terminology and Muma's (1951) subsequent modifications represent major steps toward standardization of the terminology for dentition, the many inconsistent, often contradictory usages increased confusion and reduced communication. To this day, the absence of any synthesis of these subtle changes in terminology makes it difficult to correctly interpret or compare the dentition among solifuge taxa. Perhaps for this reason, past workers on the Old World solifuge fauna (e.g., Hirst, 1911a; Hewitt, 1919b; Birula, 1937a; Turk, 1960; Levy and Shulov, 1964; Lawrence, 1955; 1968; Wharton, 1981; Reddick et al., 2010) partially or entirely ignored the terminology of Kraepelin (1899, 1901) and Muma (1951). Instead, as with earlier workers (e.g., Birula, 1890; Pocock, 1895; Pavesi, 1897; Purcell, 1903a; Mello-Leitão, 1924), no homology, implicit or explicit, was inferred for the cheliceral dentition, and only general descriptions presented (Reddick et al., 2010), sometimes numbering each tooth from distal to proximal, irrespective of size (e.g., Wharton, 1981). Overt avoidance of terminology may remove assumptions from descriptions, but results in a loss of information about homology and reduced comparability among teeth of the same or different individuals. For example, the third tooth in the median series of one species (or even an individual) is not necessarily homologous to the third tooth in another species (or individual). Many studies provide no descriptions of dentition whatsoever and refer only to figures (e.g., Lawrence, 1955, 1968; Lamoral, 1972, 1974), which may be misleading and fail to satisfactorily represent important details such as position, size, and extent of sclerotization.

The absence of a standardized terminology can largely be attributed to the absence of explicit criteria for identifying the respective teeth and precisely defined terminology for their description and communication. The aims of the study of dentition presented below are to propose hypotheses of dental homology, based on objective criteria, and to revise and standardize the terminology of Kraepelin (1899, 1901) and Muma (1951) in light of these hypotheses.

Dentition Terminology

Conserved dentition, historically referred to as “unmodified” and presumed to be plesiomorphic (Hewitt, 1919b; Wharton, 1981), refers to the pattern in plate 22B. These terms continue to be used in the present contribution merely to refer to a specific pattern of dentition and remain statements of primary homology. De Pinna’s (1991) criteria of similarity, applied to other cheliceral characters in the present contribution, were refined for primary homology assessment of dentition (table 7). “Reduced” or “absent” teeth refer to variation in the size and presence of teeth among chelicerae, and not to loss or damage by wear or deformity.

Discussions of terminology are mostly concerned with unmodified to weakly modified, i.e., conserved, patterns of dentition (pl. 22). Solifuge dentition may be divided into series, i.e., median and fondal series on the fixed finger, and median and prolateral series on the movable finger (pl. 1A, C; table 6). Each of these may be further subdivided. The fixed finger bears a single row of median teeth, which usually comprises primary and secondary teeth, and two short converging rows of fondal teeth that, in Eremobatidae, Galeodidae, and Rhagodidae, are often connected by a third, weakly developed row along the basal fondal margin. The movable finger bears a single row of median teeth, again comprising primary and secondary teeth, and a **movable finger prolateral series** (pl. 1C), in most species represented only by a carina, which varies from very weak or absent, as in Hexisopodidae, to well developed, as in Rhagodidae, to terminating distally in a tooth, as in Ammotrechidae. Muma’s (1951) terminology is modified in the present contribution as follows: “proximal” replaces “principal”; “distal” replaces “anterior” on fixed finger; “medial” replaces “anterior” on movable finger; and “secondary teeth” replaces “intermediate teeth.” “Retrolateral” and “prolateral” replace “ectal” and “mesal,” respectively. “Proximal” and “distal” replace “posterior” and “anterior,” respectively. “Proximal tooth” replaces “principal tooth” in order to describe its position. The distalmost tooth of the movable (ventral) finger is termed the “medial tooth,” to match the medial tooth on the fixed (dorsal) finger, with which it may be serially homologous. “Terminal tooth” is introduced for the tip of each finger. “Primary teeth” is introduced to refer to the three and two most prominent teeth in the median series of the fixed and movable fingers, respectively. “Secondary teeth” replaces “intermediate teeth” to complement the term “**primary teeth**.” Additional terms, i.e., “subterminal,” “subdistal,” “submedial,” and “subproximal,” are proposed to distinguish among the **secondary teeth**.

Median Series: Two median series are recognized, each comprising a single row, usually of primary and secondary teeth, on the gnathal edges of the fixed and movable fingers. Primary teeth are distinctly differentiated (larger and often more sclerotized), and comprise two teeth on the movable and three on the fixed finger (pls. 21, 22 A–D). Primary teeth on the fixed and movable fingers are often similar, e.g., the proximalmost primary tooth is the largest on each finger in most taxa, although the second proximalmost primary tooth may sometimes be the largest (e.g., in Hexisopodidae). Opposing teeth on the fixed and movable fingers are therefore hypothesized to be serial homologs, and are named accordingly. The primary teeth of the fixed finger comprise the **fixed finger proximal (FP) tooth**, i.e., the "principal tooth" of Pocock (1889), Kraepelin (1899, 1901) and Muma (1951); the **fixed finger medial (FM) tooth**, i.e., the "second" anterior tooth of Kraepelin (1899, 1901); and the **fixed finger distal (FD) tooth**, i.e., the "first" or distalmost, "anterior tooth" of Kraepelin (1899, 1901) and the "anterior tooth" of Muma (1951). The primary teeth on the movable finger comprise the **movable finger proximal (MP) tooth**, i.e., the "principal tooth" of Kraepelin (1899, 1901) and Muma (1951), and the **movable finger medial (MM) tooth**, i.e., the "anterior tooth" of Kraepelin (1899, 1901) and Muma (1951). The tips of the fingers are the terminal teeth, i.e., the **fixed finger terminal (FT) tooth** and the **movable finger terminal (MT) tooth**. Secondary teeth, i.e., the "intermediate teeth" of Kraepelin (1899, 1901), collectively refers to the less differentiated (smaller, often less sclerotized) teeth. Three categories of secondary teeth are usually present and named based on their position relative to the primary teeth: **fixed finger subdistal (FSD)**, **fixed finger submedial (FSM)** and **movable finger submedial (MSM) teeth**, situated proximal to the FD, FM, and MM teeth, respectively (pls. 21, 22). There is a broad correlation between the number of FSM and MSM teeth. For example, a single FSM tooth and a single MSM tooth are present in most taxa (e.g., Gylippinae, pl. 85C–F; most Daesiidae, pls. 136–145), but two FSM and MSM teeth are common in female Eremobatidae (e.g., females in pls. 65–83). Although there is considerable intraspecific variation in the number of FSM and MSM teeth among Galeodidae, more FSM and MSM teeth are generally present than in other families. Secondary teeth are absent on both fingers in Rhagodidae. Multidentate taxa (see section on Denticles, Multidentate Condition, Supernumerary Teeth) often possess additional secondary teeth situated proximal to the MP tooth, and proximal to the FT and MT teeth (i.e., on the fixed and movable finger mucra), and are therefore referred to as the **movable finger subproximal (MSP) teeth**, **fixed finger subterminal (FST) teeth**, and **movable finger subterminal (MST) teeth**, respectively (pls. 22D, 158F). In the present contribution, an operational assumption, supported by dentition patterns, was applied, according to which subproximal teeth are absent on the fixed finger (see section on Fondal Series, Fixed Finger).

Fondal Series, Fixed Finger: Fondal teeth are situated on the fond, the slight broadening at the base of the fixed (dorsal) finger (pls. 2A, B, 22E, F), proximal to the median series of teeth. Up to three rows of fondal teeth may be present (pls. 21, 22) within the fixed finger fondal series. Two rows diverge distally (Kraepelin, 1901; Roewer, 1934: 58), i.e., the **profondal (PF) teeth**, corresponding to Muma's (1951) mesal row, and the **retrofondal (RF) teeth**, corresponding to Muma's (1951) ectal row. The basifondal (BF) teeth, situated along the basal margin of the fond, are usually minute, and present only in Eremobatidae (pl. 84I, J), Galeodidae (pl. 64K, L), and Rhagodidae (pl. 64I, J). Muma (1951) numbered the fondal teeth from distal to proximal with Roman numerals (Muma, 1951: 38, fig. 5), a convention followed by Brookhart (e.g., 1965) and Brookhart and Cushing (e.g., 2002, 2004). This numbering was not intended to reflect homology, i.e., the same numerals assigned to teeth in different taxa did not imply that these teeth were homologous.

The profondal (PF) row generally comprises one to four teeth (pls. 21, 22E, F, 23L). An additional, minute fifth tooth is occasionally present,

TABLE 6

Synonyms for dentition of Solifugae used in the literature

Asterisk indicates teeth commonly included with anterior teeth in literature.
Abbreviations: **FF,** fixed finger; **MF,** movable finger.

		Kraepelin (1901)	Muma (1951)	Other authors
median series (FF, MF)	**primary teeth**			*canines* (Dufour, 1861)
	FF, distal (FD) tooth	*Vorderzähne**	anterior tooth	anterior teeth* (Maury, 1970, 1982; Rocha and Carvalho, 2006); anterior tooth 1 (Fa_1) (Botero-Trujillo, 2014)
	FF, medial (FM) tooth	*Vorderzähne**	medial tooth	anterior teeth* (Maury, 1970, 1982; Rocha and Carvalho, 2006); anterior tooth 3 (Fa_3) (Botero-Trujillo, 2014)
	FF, proximal (FP) tooth	*Hauptzahn*	principal tooth	principal tooth (*Fp*) (Botero-Trujillo, 2014)
	MF, medial (MM) tooth	*Vorderzähne*	anterior tooth	anterior tooth (*Ma*) (Botero-Trujillo, 2014)
	MF, proximal (MP) tooth	*Hauptzahn*	principal tooth	principal tooth (Pocock, 1889); primary tooth (Brookhart and Cushing, 2004, 2008; Catenazzi et al., 2009); principal tooth (*Mp*) (Botero-Trujillo, 2014)
	secondary teeth			*incisives* (Dufour, 1861)
	FF, subterminal (FST) tooth/teeth			
	FF, subdistal (FSD) tooth/teeth	*Vorderzähne**	anterior teeth	anterior teeth* (Maury, 1970, 1982; Rocha and Carvalho, 2006); anterior tooth 2 (Fa_2) (Botero-Trujillo, 2014).
	FF, submedial (FSM) tooth/teeth	*Zwissenzähne*	intermediate teeth	second principal tooth (Rocha and Carvalho, 2006); intermediate teeth ($Fi_{1, 2}$) (Botero-Trujillo, 2014)
	MF, subterminal (MST) tooth/teeth			
	MF, submedial (MSM) tooth/teeth	*Zwissenzähne*	intermediate teeth	intermediate teeth ($Mi_{1, 2}$) (Botero-Trujillo, 2014)
	MF, subproximal (MSP) tooth/teeth			
fondal series (FF)[a]	**profondal row**[b]	*mediale (innere) Wangenzähne*	mesal row	*jugales internes* (Vachon, 1950); *basal interno* (*BI*) (Maury, 1984); mesal fondal teeth (Fmf_{1-3}) (Botero-Trujillo, 2014).
	retrofondal row[c]	*laterale (äussere) Wangenzähne*	ectal row	*jugales latérales* (Vachon, 1950); *basal externo* (*BE*) (Maury, 1984)
	basifondal row			
	basifondal (BF) teeth			*Gelenksrande sitzenden Zähnchen* (Birula, 1937a)
prolateral series (MF)	MF, prolateral (MPL) tooth	*Nebenzahn*	mesal tooth	*medialen Wangenzahn* (Roewer, 1934); *dientebasal interno* (*BI*) [of MF] (Maury, 1982, 1984); median tooth (Wharton, 1981)
	MF, prolateral carina (MPLC)			
finger tips	FF, terminal (FT) tooth			
	MF, terminal (MT) tooth			

[a] Historical use includes *Wangenzähne* (Kraepelin, 1901), fondal teeth (Muma, 1951), *molaires* (Dufour, 1861), and basal teeth (e.g., Mello-Leitão, 1938; Maury, 1970, 1984; Armas, 2002).

[b] Includes profondal medial (PFM) tooth, profondal submedial (PFSM) tooth/teeth, profondal proximal (PFP) tooth, and profondal subproximal (PFSP) tooth/teeth. Usually a single PFSM tooth and a single PFSP tooth.

[c] Includes retrofondal apical (RFA) tooth/teeth, retrofondal medial (RFM) tooth, retrofondal submedial (RFSM) tooth/teeth, retrofondal proximal (RFP) tooth, and retrofondal subproximal (RFSP) tooth/teeth.

often forming a small bifid tooth at the proximal end of the PF row (pls. 21A, 78A). Two conspicuous teeth, separated by a smaller tooth or a distinct gap, the "diastema" mentioned by Maury (1976), are usually evident in the PF row. These teeth are typically narrow and pointed apically, and are often the largest (tallest) in the fondal series. They were commonly mentioned in species diagnoses, e.g., Birula (1926: 196) and Lawrence (1935: 77), but homology across the order was previously unrecognized. These teeth are referred to here as the **profondal proximal (PFP) tooth** and **profondal medial (PFM) tooth**. If present, a tooth situated between the PFP and PFM teeth, and another one or two teeth situated proximal to the PFP tooth, are referred to as the **profondal submedial (PFSM) tooth** and the **profondal subproximal (PFSP) tooth/teeth**. Two PFSM teeth are, however, very rare, and may be abnormal.

Although homologizing individual retrofondal (RF) teeth across the entire order proved challenging, probable homologs were often readily identified among putative phylogenetically related species or genera (pls. 21B, 22E, F, 23). The most prominent landmark tooth is referred to here as the **retrofondal proximal (RFP) tooth**. This tooth is situated toward the proximal end (usually subproximal) of the RF row, and can often be identified by its distinct shape (equilateral triangle with a simple, sharp point at the apex). It is also often, although not necessarily, the largest tooth in the RF row. This tooth is especially distinct in size and shape in Lipophaginae (pls. 85H, 87B, D, F, 88). By using the RFP tooth as a landmark, and by comparing taxa with distinct fondal dentition patterns, other probable homologs may be identified within the RF row (pl. 23). For example, in Solpugidae, four or rarely five retrofondal teeth are typical, often with subtle yet identifiable differences in size, and may be identified as follows (pls. 22B, E, 23Q, R, 90G–L, 103B, D): the two largest teeth, i.e., an equilateral triangular retrofondal proximal (RFP) tooth and a **retrofondal medial (RFM) tooth**, often similarly equilateral, separated by a smaller **retrofondal submedial (RFSM) tooth**, in addition to one, rarely two, proximally situated **retrofondal subproximal (RFSP) tooth/teeth**. This interpretation may be extrapolated to other taxa, e.g., the three most prominent RF teeth of Galeodidae (pls. 23M, N, 59, 64K, L) or even the three to four most pronounced RF teeth of Eremobatidae (pls. 68B, D, 84). In male Eremobatidae, the RF teeth commonly decrease in size proximally, such that the RFSM tooth is often larger than the RFP tooth, but its identity as an RFSM tooth is confirmed by comparison with females (cf. pl. 78B with D) and males of different species with a more "typical" pattern (two large teeth alternating with two smaller teeth; cf. pl. 68B with 68D).

Teeth of the fondal series (RF row) may be difficult to distinguish from possible subproximal teeth of the median series on the fixed finger, especially when more than four teeth (or five, if there are two RFSP teeth) are present proximal to the fixed finger proximal (FP) tooth, as in Eremobatidae, Karschiidae, Mummuciidae, and Rhagodidae. Muma (1951: 38, fig. 6) and some New World workers (e.g., Brookhart and Cushing, 2004: 286, for Eremobatidae; Catenazzi et al., 2009: 154, according to their dental formula for a species of Ammotrechidae) recognized an "intermediate tooth," i.e., a fixed finger subproximal (FSP) tooth in the terminology presented here, between the FP tooth and the fondal teeth. Examination of specimens indeed indicated that, in the presence of such a large number of teeth proximal to the FP tooth, some teeth situated directly proximal to the FP tooth, but on the gnathal edge, are often more similar to median teeth than to fondal teeth (e.g., pls. 21, 67D, H, L). This similarity includes level of sclerotization (e.g., in some species, teeth of the median series are more sclerotized only toward the apices whereas fondal teeth are entirely more sclerotized) and/or structure (e.g., teeth of the median series are laterally compressed whereas fondal teeth are conical in shape). The distinction is not always clear, however, and contradictory patterns may be apparent. In the present contribution, and pending further investigation, all teeth situated proximal to the FP tooth and distal to the RFM tooth are therefore regarded as part of the fondal series, referred to here as **retrofondal apical (RFA) teeth**. For example, Rhagodidae typically exhibit six or seven teeth forming a curved row, proximal to the FP tooth, generally comprising four teeth (the RFSP, RFP, RFSM, and RFM teeth) in the basal, curved part of the row, and three teeth on the gnathal edge, aligned with and directly proximal to the FP tooth, and distal to the RFM tooth (pl. 64I, J). The three teeth on the gnathal edge are structurally more similar to teeth of the median series in being somewhat laterally compressed with a distinct median edge, unlike the uniformly rounded proximal teeth, but are as sclerotized as the four proximal teeth. The three teeth on the gnathal edge are therefore also referred to as retrofondal apical (RFA) teeth. This interpretation is noteworthy as it is consistent with the absence of secondary teeth in Rhagodidae. Some retrofondal apical (RFA) teeth on the gnathal edge are structurally similar to teeth of the median series, e.g., in Karschiidae (pl. 64A–H), Mummuciidae (pl. 153I, J), and female Eremobatidae (pl. 84E, F), but again a consistent pattern could not be identified, and the term *RFA* was therefore applied. According to this hypothesis, and pending further investigation, small teeth (denticles) in the fondal notch of male eremobatids are RFA teeth (pl. 84G, H). Retrofondal apical teeth appear to be absent in, e.g., Ammotrechidae, Daesiidae, and Solpugidae (pl. 23).

In addition, one or more small to minute teeth are often present at the proximal end of the PF and RF rows, merging with the basal fondal margin, and providing it with a serrate edge in some taxa (e.g., Muma, 1951: 39). Such apparently vestigial teeth blur the distinction between the presence or absence of proximally situated PF and RF teeth, and contribute to inflated estimates of variation in the number of fondal teeth. Panouse (1964) recognized the dilemma regarding whether to include denticles on the basal fondal margin within counts of the PF and RF rows, reluctantly following previous authors by excluding them. According to Panouse (1964: 51, fig. 1, 2D, E), however, the PF and RF counts would be stable among the four known species of *Othoes* Hirst, 1911, even if these teeth were included. In the present study, examination of different conspecifics usually permitted identification of such vestigial teeth as either RFSP or PFSP teeth, or as crenulation fused with the basal fondal margin and therefore excluded from PF and RF counts.

The retrofondal (RF) row gradually merges with the median series and some workers (e.g., Birula, 1926: 192–3, fig. 1b; Lamoral, 1974: 267, fig. 1) regarded these teeth as a single unit, i.e., the "external row" or "outer teeth."

The basifondal (BF) teeth represent a third row of vestigial teeth, applied to teeth situated on the basal fondal margin, which do not form part of either the PF or RF rows (e.g., Aliev, 1985: 1101, fig. d). Basifondal teeth have been observed in Galeodidae (pl. 64K, L; Sørensen, 1914; Roewer, 1934: 53) and Rhagodidae (pl. 64I, J; Pocock, 1889; contra Roewer, 1934: 54), whereas weak BF teeth may be present in Eremobatidae (pl. 84I, J).

Regularly arranged rows of beadlike denticles at the base of the fond (fig. 2A, pls. 2A, 131) constitute a potential synapomorphy for Hexisopodidae. These denticles may be homologous with the basifondal (BF) teeth as suggested by their partial merger with the basal fondal margin, which resembles teeth in the BF row, or may have originated from the proximalmost PF and RF teeth, which subsequently shifted medially along the fondal margin. The latter hypothesis is supported by similar patterns observed in Eremobatidae (pl. 84I, J), Gylippinae (pl. 90A, B), and Karschiidae (pl. 64C, D) in which the proximalmost teeth are denticlelike, often beadlike, and situated on the pro- and retrolateral ends of the basal fondal margin to form crenulations at

TABLE 7

Criteria for primary homology assessment of median series dentition in Solifugae

Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth.

1. Structural; size and level of sclerotization: Primary teeth more differentiated (larger and darker) than secondary teeth.
   Corollary 1: Secondary teeth lost or reduced before primary teeth.
   Corollary 2: Primary teeth lost distal to proximal.
   Corollary 3: Within-category[a] secondary teeth lost in order of subordinate to principal (small to large).
2. Positional; relative to other primary teeth on finger: Movable finger: MP tooth = proximalmost; MM tooth = distalmost. Fixed finger: FP tooth = proximalmost, first tooth distal to fondal teeth; FM tooth = first primary tooth distal to FP; FD tooth = distalmost.
3. Positional; relative to serial homolog on opposing finger: FP tooth closes directly distal to MP tooth, and FM tooth distal to MM tooth.
4. Corroboration between sexes and among taxa; similarities in dental pattern and structures (e.g., flanges) between sexes and among putatively related species.

[a] Category of secondary teeth refers to FSD, FSM and MSM teeth.

the proximal base of the fondal rows. The beadlike teeth are not on the margin itself (pl. 131C, D) as, e.g., in Galeodidae (pl. 64K, L). Furthermore, in Hexisopodidae, more beadlike denticles are present on the retrolateral surface than on the prolateral surface, as is often the case with the pro- and retrolateral fondal teeth. The beadlike denticles of Hexisopodidae are therefore considered here to be pro- and retrofondal (PF and RF) teeth rather than basifondal (BF) teeth, and possibly homologous to the pro- and retrofondal crenulations situated proximally at the base of the respective fondal rows of, e.g., Eremobatidae.

The distinction among the various fondal teeth, more obvious in some taxa than others, is critically important to evaluate variation in fondal teeth. Similarly, the identification of homologous teeth in the PF and RF rows among taxa varies in difficulty and may, in some cases, be impossible with the data and specimens available. Hypotheses for the most typical RF patterns in major suprageneric taxa are proposed in plate 23. Such hypotheses were based on relative size, level or pattern of sclerotization, and comparison among related taxa. Further examination and comparison of an adequate number of specimens of related taxa is, however, necessary to test the proposed hypotheses concerning the homology of fondal teeth.

Prolateral Series, Movable Finger: The prolateral series of the movable finger comprises a **movable finger prolateral tooth (MPL)** and a **movable finger prolateral carina (MPLC)** (pl. 1C). The MPL, a basal tooth on the prolateral surface of the movable finger (pls. 15B, 22C), situated slightly below the movable finger primary (MP) tooth, was reported in Ammotrechidae (Roewer, 1934: 54; Muma, 1951; Armas, 1994), Eremobatidae (Muma, 1951), Rhagodidae (Roewer, 1934: 54), and several species of Solpugidae (Lawrence, 1954; 1961; Roewer, 1934: 429; Wharton, 1981). The MPLC is a weakly to markedly developed longitudinal carina present in place of, or in addition to, an MPL tooth, from which it may extend proximally (pls. 1C, 58B). The distinction between a tooth and a pronounced carina is a continuum and they are hypothesized to represent states of a single character. Brookhart and Muma (1981) considered the size of the prolateral tooth to be useful, in combination with other characters, for species identification.

Category-specific Size Gradation: When two or more teeth are present within a category of secondary (i.e., FSM, FSD, and MSM) teeth, the teeth may progressively decrease in size, proximally or distally (fig. 17, table 8). These patterns are significant for homology assessment of secondary teeth. Different gradations in each category appear to be taxon specific and may prove synapomorphic, especially at the family level (pls. 24, 25; table 8). For example, Eremobatidae is the only family in which the teeth of all three categories (i.e., FSM, FSD, and MSM) increase in size proximally (pl. 24O). The only apparent deviation, rarely observed, concerns species possessing more than the usual number of teeth in a category for that family or subfamily, due to the presence of small teeth, usually denticles, between the secondary teeth, e.g., three small teeth interspersed in the FSM row in *Solpugiba lineata* (fig. 17B, pls. 110B, 111B), or a minute third denticle between two larger FSD teeth in *Horribates bantai* Muma, 1989 (fig. 17A). These denticles, the most labile of all teeth in size and presence or absence, should be ignored when assessing gradation patterns (fig. 17A, B). For example, a small but distinct proximalmost FSM tooth (pl. 110A, B) that appeared to confuse gradation patterns in adult *S. lineata*, was found to be misleading when 10 juvenile specimens were examined: the tooth was absent in 18 of the 20 juvenile chelicerae, which were therefore consistent with an FSM gradation pattern of decreasing size distally.

Denticles, Multidentate Condition, Supernumerary Teeth: The terms "denticles," "multidentate," and "supernumerary" are commonly encountered but inconsistently applied in the literature. "**Denticle**" has been used as a synonym for "tooth" (primary, secondary, and fondal teeth; Birula, 1926), to describe the small teeth typical of the multidentate condition (Wharton, 1981), e.g., in *Lawrencega*, or to describe very minute, often intraspecifically variable teeth, as used here. For example, the movable finger of the male *Lawrencega procera* Wharton, 1981 (pl. 154I, J) possesses a row of minute teeth (i.e., denticles) distal to a row of small, similar teeth, not denticles. Most denticles are secondary or fondal teeth.

"**Multidentate**," subjectively applied in the literature, is defined here in accordance with the most common usage, to describe a pattern of dentition characterized by a row of small, similar, equally spaced teeth in the median series, with relatively homogeneous teeth in the median and retrofondal series (pls. 24R, 154J, L, 158). Compared to taxa that exhibit "typical" dentition, taxa that exhibit the multidentate condition possess more secondary teeth, and the gnathal edges of the fingers tend to be sublinear, resulting in a row of small, relatively homogeneous teeth with the pattern of gradation absent or weakly expressed. The multidentate condition occurs predominantly in Melanoblossiinae and, to a lesser extent, Karschiidae. It may be restricted to only one sex or to one cheliceral finger.

The dentition of some species of Eremobatidae, Karschiidae, Melanoblossiinae, and Mummuciidae, usually females, exhibit some multidentate characters, e.g., an increased number of secondary teeth, crenulations on the mucron (FST and MST teeth) and proximal to the movable finger median series (MSP teeth), and greater homogeneity among all teeth of the median series (pls. 24O, P, 50H, 70J, 149H, 154C), but cannot be described as truly multidentate based on the aforementioned definition. In *Eusimonia divina* Birula, 1935, the fixed fingers of both sexes are multidentate but more distinctly so in males, in which the primary and secondary teeth are similar in size and regularly spaced, whereas the movable finger of the female only presents a tendency toward the multidentate condition, with greater differentiation in size between the primary and secondary teeth (pl. 53G–J). Wharton (1981) described the dentition of *Namibesia pallida* (pls. 132A–D, 133), which possesses an unusually large number of secondary teeth compared to other daesiid taxa, as multidentate. However, this species does not possess the multidentate characteristics redefined here, e.g., the teeth are not similar and equally spaced, and it is therefore not regarded as multidentate. *Namibesia pallida* simply possesses more than the usual number of FSD and

FSM teeth, just as Galeodidae possess more than the usual number of MSM teeth. Multidentate patterns of dentition, and a tendency toward such patterns, occur in taxa as diverse as Eremobatidae, Karschiidae, Melanoblossiinae, and Mummuciidae, and are sometimes more pronounced in one sex or the other. Taxa with a tendency toward this pattern of dentition may provide useful insights into its evolution.

"**Supernumerary**," defined as "exceeding the usual, stated, or prescribed number" (Grove, 1986: 2295), has been used to refer to various structures: the movable finger prolateral (MPL) tooth (Brookhart, 1965: 153); denticles situated among the fondal teeth (Muma, 1962: 11) or in the fondal notch of Eremobatidae (Brookhart and Muma, 1981: 302, fig. 73); the flagellar groove process (FGP) near the tip of the finger of some Solpugidae (vide Pocock, 1897); additional secondary teeth indicating an abnormality (Fichter, 1940: fig. 1G, H), bilateral asymmetry (e.g., Muma, 1951: 50), intraspecific variation (e.g., Muma, 1962), and interspecific variation in the median series (e.g., Muma, 1962: 10); or the retrolateral fondal series (e.g., Maury, 1980b). The use of "supernumerary" is unnecessary, however, if the aforementioned structures and "additional" teeth are more precisely defined, e.g., prolateral tooth, denticle-sized subproximal teeth, etc.

Numbering of Teeth and Dental Formulae

Numbers and formulae are commonly used to describe the dentition of solifuges. A distal to proximal numbering is conventionally used in place of terms for individual teeth (e.g., Wharton, 1981). Two types of **dental formulae** are used, i.e., a dental pattern formula (tables 9, 10) and a size grading formula. Unfortunately, dental formulae have not been standardized.

Dental Pattern Formulae: Dental pattern formulae employ a combination of dental terms and numbers to indicate the types of teeth, and the number of each. Several formulae are currently in use (table 9). A standardized formula, which incorporates variation in the secondary and fondal teeth, is proposed here. Notation for the fixed (dorsal) finger dentition of *Uspallata* cf. *pulchra* (pls. 26, 152) is FD-(1)-FM-($\underline{1}$-2)-FP-(5-$\underline{7}$RF)(3?PF). Numbers in parentheses indicate secondary (FSD and FSM) and fondal (RF and PF) teeth, ranges indicate variation (when applicable), underlined numbers indicate the most common pattern, and question marks indicate uncertainty, e.g., when teeth are obscured or a tooth or part of the chelicera is broken. Notation may be adapted to accommodate different patterns and levels of understanding, e.g., (2,$\underline{3}$,4RF), or (PFM-0,$\underline{1}$-PFP-1).

Size Grading Formulae: Two superficially similar yet fundamentally different size-grading formulae are used, illustrated here with the profondal (PF) teeth of plate 22C as an example. The first formula for grading fondal teeth was introduced by Muma (1951), and followed by Brookhart (1965) and Brookhart and Cushing (2002, 2004, 2008). According to this system, individual fondal teeth are numbered from distal to proximal with Roman numerals, and then ordered from large to small. The notation I-III-IV-II for the PF teeth in plate 22C thus indicates that the first tooth is the largest, followed by the third, fourth, and second, respectively. This formula does not allow for coding teeth of similar size, however, which requires elaboration in the text, e.g., "FT graded I, III, II, IV, FT III…large as FT I" (Brookhart and Cushing, 2004: 290). The second system (Maury, 1982) used Roman or Arabic numerals to indicate the relative sizes of teeth, e.g., Roman numerals for median and fondal teeth (Xavier and Rocha, 2001; Rocha and Cancello, 2002; Rocha and Carvalho, 2006; Carvalho et al., 2010) or Arabic numerals for fondal teeth only (Maury, 1982; Armas, 1993). Teeth are referred to in decreasing order of size, from distal to proximal, with size I (or 1) being the largest, size II (or 2) the second largest, and so on, in the order in which they are situated on the finger. According to this system, the notation for the PF teeth (pl. 22C) would be I-IV-II-III (or 1-4-2-3) as opposed to I-III-IV-II in the notation of Muma (1951). This system assigns the same notation to teeth of similar size, e.g., II-I-III-I indicates that the second and fourth teeth are of similar size, and is therefore preferred here.

Size-grading formulae are prone to error and subjectivity, and comparison between the median and fondal series is complicated by different shapes, but may be of value for independently communicating relative size, especially regarding line drawings, which are often misleading in size. For example, in the study by Carvalho et al. (2010), the retrolateral fondal teeth grading of I-III-V-II-IV does not match the line drawing (Carvalho et al., 2010: 23, fig. 9), but appears to match the scanning electron micrograph (Carvalho et al., 2010: 25, fig. 15). The size-grading formula thus added a level of accuracy to the species diagnosis of Carvalho et al. (2010). It is suggested here that Arabic numerals (1, 2, 3, etc.) should be reserved for individual teeth, e.g., for distinguishing among multiple secondary teeth within a category, such as three MSM teeth, similar to the subscript notation of Botero-Trujillo (2014), leaving Roman numerals (I, II, III, etc.) for ranking size.

Life Stages and Sexual Dimorphism

The cheliceral dentition of females and juveniles is more conserved (Hewitt, 1919b), and the dentition of females often more worn (Fichter, 1940), than that of males. Reliably identified immature specimens are rare but, based on those that were examined, the dentition of immatures appears to be similar to that of females, except sharper and more pronounced, probably due to less wear. For example, in *Zeriassa*, the FM tooth is usually larger than the FD and FP teeth (pl. 124E, H), a pattern exaggerated in immatures (pl. 124F).

Modifications to the dentition increase with each molt in immature males. Based on an examination of six males, one female, and six immatures, Wharton (1981) documented the change with each molt from the distal (FD) and medial (FM) teeth on the fixed finger being similar in size and shape among immature *Biton* (*B.*) *striatus* (Lawrence, 1928), to the forms and shapes observed in adult males. Secondary teeth appear to be added as specimens mature. Birula (1926: 182) reported the absence of secondary teeth on the chelicera of "a…number of young specimens" of *Galeodes arabs* C.L. Koch, 1842. In the present investigation, fewer secondary teeth, especially "labile denticles," were identified in juvenile *Solpugiba lineata* than in adult conspecifics.

Taxonomic Significance and Intraspecific Variation in Dentition

It is well known in systematics that interspecific variation is informative for species delimitation and diagnosis, whereas intraspecific variation contributes noise. Dentition is commonly used in solifuge taxonomy, but simultaneously criticized for unreliability. Variation in dentition, especially intraspecific, remains poorly understood.

Historical Perspective: Cheliceral dentition has traditionally been used for solifuge systematics at all levels (Kraepelin, 1901; Birula, 1905; Hewitt, 1919b: 12; Lawrence, 1955; Muma, 1970a; Wharton, 1981; Maury, 1982, 1984) but the influential monograph of Roewer (1934) placed the greatest emphasis on this character system. Roewer (1934: 55, 509) considered dentition to be constant intraspecifically and emphasized its importance in solifuge systematics. Roewer (1934: 509) treated any variation in dentition not attributable to wear or damage as a diagnostic character, as reflected in almost every species-level identification key to solifuges presented. Faced with an increasing number of species and genera that could not be accommodated within Roewer's (1934) classification, subsequent workers began to doubt the stability of solifuge dentition and criticized Roewer's (1934) reliance on characters that are highly variable (e.g., Birula, 1936b; Simonetta and Delle Cave, 1968; Turk, 1960). Some species diagnosed by Roewer

(1934) on the basis of dentition were subsequently synonymized (e.g., Gromov, 2000) but, for the majority of taxa, Roewer's (1934) classification prevails. Regardless of reservations concerning the value of dentition for solifuge systematics, there is general recognition that taxon-specific patterns are real, reflected by statements such as "dentition is comparatively constant within limits of any one form" (Hewitt, 1919b: 14), "dentition...apparently quite variable but in general as in...paratype" (Muma, 1962: 12), "dentition of chelicerae somewhat variable but maintaining general pattern" (Muma, 1963: 2), "dentition…cannot be relied upon exclusively for generic or specific distinctions…this does not exclude their use entirely, as long as variation is taken into consideration" (Wharton, 1981: 71), and dentition is "generally species-specific" (Rocha and Carvalho, 2006: 166). The urgent need to reevaluate inter- and intraspecific variation in solifuge cheliceral dentition depends on series of adult males and females, accurate identifications, and comparability among studies.

Roewer's (1934) emphasis on stable dentition is probably an artifact of small sample sizes, a problem that continues to hinder solifuge taxonomy (Turk, 1960; Wharton, 1981). Variation cannot be satisfactorily assessed without the availability of many specimens, especially adults, ideally from the same series (collection event). Solifugae are rarely collected in large series, however (Hewitt, 1919b; Dean and Griffin, 1993; Brookhart and Cushing, 2004), and even when large series are available, variation is rarely quantified, and the number of specimens designated as types is often a subset of the number collected.

Evaluations of intraspecific variation are reliable only when based on accurately identified specimens. Unfortunately, identifications are often uncertain, especially among Old World solifuges (see Harvey, 2002b) for several reasons. Descriptions of genera and species are often inadequate and sometimes contradictory (Simonetta and Delle Cave, 1968; Lawrence, 1968; Rocha, 2002). For example, see discrepancies, especially concerning the flagellum and

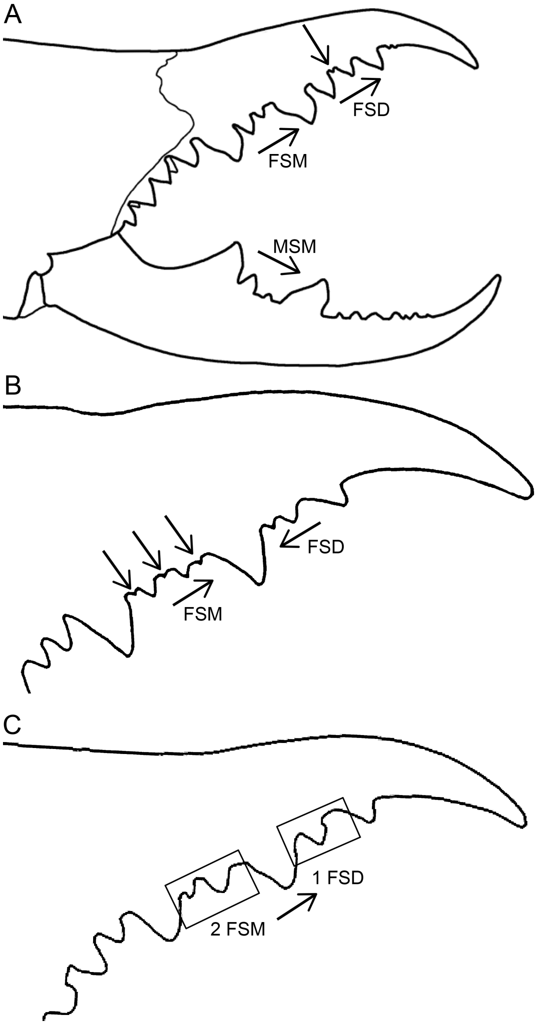

FIG. 17. Eremobatidae Kraepelin, 1899 (**A**), Solpugidae Leach, 1815 (**B**), and Galeodidae Sundevall, 1833 (**C**), chelicera (**A**) and fixed finger (**B, C**), retrolateral views, indicating patterns of size gradation (**A, B**), and decreasing number of FSM to FSD teeth (**C**). **A.** *Horribates bantai* Muma, 1989, ♀ (DMNS ZA.17691). **B.** *Solpugiba lineata* (C.L. Koch, 1842), ♀ (AMNH [LP 5919]). **C.** *Galeodes araneoides* (Pallas, 1772), ♀ (AMNH), Turkey: Gurgen. Arrows oriented parallel to teeth indicate gradation patterns; arrows pointing to teeth indicate labile denticles inconsistent with gradation patterns and consequently ignored. Abbreviations: **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **MSM,** movable finger, submedial teeth.

TABLE 8

Size gradation within categories of secondary (FSD, FSM, and MSM) teeth in Solifugae

Based on material examined as well as images and species diagnoses from the literature, indicating whether teeth increase in size distally or proximally within a row. "n.a." denotes taxa with fewer than two teeth in a category, or more than one tooth only in apparently abnormal specimens and/or insufficient data, which therefore could not be evaluated for size gradation.

Abbreviations: **D,** distally; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **MSM,** movable finger, submedial teeth; **P,** proximally.

Family	FSD	FSM	MSM
Ammotrechidae Roewer, 1934	n.a.	n.a.	n.a.
Ammotrechidae (*Sedna* Muma, 1971)[a]	n.a.	P	P
Ceromidae Roewer, 1933	n.a.	n.a.	n.a.
Daesiidae Kraepelin, 1899 (*Namibesia* Lawrence, 1962)	P	D	n.a.
Daesiidae (excl. *Namibesia*)	n.a.	n.a.	n.a.
Eremobatidae Kraepelin, 1901	P	P	P
Galeodidae Sundevall, 1833[b]	n.a	P	D
Gylippidae Roewer, 1933	n.a.	n.a.	n.a.
Karschiidae Kraepelin, 1899	P	P	D
Melanoblossiidae Roewer, 1933[c]	n.a.	n.a.	n.a.
Mummuciidae Roewer, 1934[d]	n.a.	P	P
Rhagodidae Pocock, 1897	n.a.	n.a.	n.a.
Solpugidae Leach, 1815[e]	n.a.	P	P

[a] Single MSM tooth according to Muma (1971: 7, figs. 1, 2).

[b] Contradictory pattern of FSM teeth in *Galeodes araneoides* (Pallas, 1772) (pl. 59I, J).

[c] Teeth either too small and vestigial to evaluate for relative size, or all teeth within series of equal size (i.e., multidentate patterns).

[d] e.g., *Mummucina titschacki* Roewer, 1934 (vide Botero-Trujillo, 2014: 325, fig. 17).

[e] Labile denticles interspersed with "regular" secondary teeth ignored in *Solpugiba* Roewer, 1934.

dentition, in the descriptions of *Biton* (*B.*) *subulatus* by Purcell (1899: 389, fig. 12) and Roewer (1934: 389, fig. 275f_1). Type designations are often unclear and/or inadequate, e.g., the description of *Zeria toppini edentula* (Lawrence, 1937), based on a male with excessively worn teeth (Lawrence, 1937: 265, fig. 27a), types lost or untraceable, and the depositories unspecified (e.g., Muma, 1951, Simonetta and Delle Cave, 1968). Females or immatures, lacking relevant diagnostic characters, have often been designated as holotypes, and may be impossible to associate with adult male conspecifics (Turk, 1960; Simonetta and Delle Cave, 1968). Type localities are often vaguely defined and impossible to locate (Turk, 1960; Simonetta and Delle Cave, 1968). There are few revisionary syntheses.

Even when notes on variation in dentition are provided, the literature may be of limited comparative value, for several reasons. Different interpretations and terminology, such as whether a structure is interpreted as a flange or as one of the regular teeth, and whether or not a denticle is counted as a tooth (e.g., Simonetta and Delle Cave, 1968), reduce comparability among or even within studies. Different interpretations may have taxonomic implications, affecting how intraspecific variation is evaluated. For example, Lawrence (1949b) separated *Chelypus kalaharicus* Lawrence, 1949 from *C. hirsti*, based mainly on differences in the number of teeth on the fixed (dorsal) finger. When Lamoral (1973: 95) reexamined the holotype, identified as "definitively a juvenile or subadult male" (despite the presence of a flagellum), two denticles, not mentioned by Lawrence

TABLE 9

Dental pattern formulae of Solifugae according to the literature and a newly proposed formula

Formulas adapted to describe dentition pattern illustrated in plate 22A with hypothetical presence of additional third fixed finger submedial (FSM) tooth and one retrofondal (RF) tooth present or absent, depending on specimen Abbreviations: **A,** *anterior*; **AT,** anterior teeth; **BE,** *basal externo*; **BI,** *basal interno*; **DA,** *dent antérieure*; **DI,** *dent intermédiaire*; **DJ'ext,** *dent jugale externe*; **DJ'int,** *dent jugale interne*; **DP,** *dent principale*; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **I,** *intermedio*; **M,** medial teeth; **P,** *principal*; **PF,** profondal teeth; **RF,** retrofondal teeth.

Dental formula	Reference
3DA+2DI+1DP+5DJ'ext+4DJint	Panouse (1960b)
3A, 2-3I, 1P, 5BE, 4BI[a]	Maury (1984, 1985)
3A, 2I, 1P, 5BE, 4BI	Armas (1993)
PT-1-2-MT-1-AT (alternating with P-1-2-M-1-A)[b]	Catenazzi et al. (2009)
FD-(1)-FM-($\underline{2}$-3)-FP-(4-5RF)(4PF)[c]	present contribution

[a] 2-3I = intraspecific and/or individual variation in count of submedial (FSM) teeth.

[b] 1-2: implies two submedial teeth, respectively numbered "1" and "2"; Catenazzi et al. (2009) cited Maury (1982) but probably based on Maury (1984), with modifications.

[c] ( ) = secondary teeth and fondal teeth; ($\underline{2}$-3) = variation, intraspecific and/or within specimen, in count of secondary teeth; predominant count underlined. Notation may be adapted to accommodate different patterns of variation, e.g., (2,$\underline{3}$,4).

(1949b), were identified, on the basis of which *C. kalaharicus* was synonymized with *C. hirsti*. Lawrence (1949b) may not have regarded the denticles as taxonomically significant.

Lastly, only a handful of studies report variation in a manner that enables the identification of interspecific, intraspecific, or even intrapopulation variation, e.g., by reporting variation among individuals (e.g., Simonetta and Delle Cave, 1968; Lamoral, 1973) or within populations (e.g., Wharton, 1981; Botero-Trujillo, 2014). The few studies that report variation in detail (e.g., Maury, 1976: 94, 95), often including basic statistics (e.g., Simonetta and Delle Cave, 1968; Wharton, 1981), were intended for general descriptions of intraspecific variation, rather than for comparisons of specific teeth within and among taxa. Nonetheless, it is often possible to use such data to assess which broad categories as well as types (e.g., size) of teeth are more prone to variation within individuals (table 11) and populations (table 12).

False Interpretation of Variation: Worn and damaged teeth, especially in older females and fossorial taxa (e.g., Lawrence, 1963: 5, fig. 4; Wharton, 1981), are easily misinterpreted as small or absent teeth. Aberrant teeth may also be mistaken for intrinsic variation. Solifuges appear to have a propensity for abnormalities, e.g., flagellum lost (Turk, 1960: 115) or duplicated (Wharton, 1981: 30) on one chelicera, a double unguis, or a deformed leg (e.g., Roewer, 1934: 255), and dentition is no exception. Variation in dentition is seldom as obvious as the presence of a duplicate flagellum, but just as the latter abnormality would not be indicative of variation in number of flagella on a chelicera, aberrant teeth should not be counted as intrinsic variation. Examples of aberrant teeth include a bifid FM tooth in a female *Melanoblossia braunsi* Purcell, 1903 (pls. 154C, 155F) and a bifid FD tooth reported by Simonetta and Delle Cave (1968) in a specimen of *Solpuga* Lichtenstein, 1796, each restricted to a single chelicera. Other examples involve all teeth on the chelicera, again with some examples more clearly aberrant than others. A striking example is the "distinctive" chelicerae characterized by peculiar teeth, including the apex of the finger, on the basis of which Turk (1948: 269) diagnosed the female of *Solpugella asiatica* Roewer, 1933, but which is undoubtedly a chelicera with highly worn teeth (fig. 18A). It is less certain whether, e.g., the dentition of the single specimen of a putative *Ferrandia robusta* Lawrence, 1954, examined in the present study

TABLE 10

Common dentition patterns in families of Solifugae, excluding highly modified male dentition

Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth/teeth; **FSM,** fixed finger, submedial tooth/teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **MSP,** movable finger, subproximal tooth; **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth; **STF,** subterminal flange. Parentheses indicate secondary teeth and fondal teeth. Ranges indicate predominant intraspecific variation. Underlining indicates most common pattern. Only general patterns, not minor intraspecific variation, indicated.

	Fixed finger	Movable finger
Ammotrechidae Roewer, 1934[a]	FD-(0,1)-FM-(1,2)-FP-(3,4RF)	MM-(0,1,2,3)-MP
Ceromidae Roewer, 1933 (excl. *Toreus* Purcell, 1903)	FD-FM-(0,1)-FP-(2-5RF)	MM-(0,1)-MP + 2 flanges
Daesiidae Kraepelin, 1899 (*Namibesia* Lawrence, 1962)[b]	FD-(1,2,3)-FM-(1,2)-FP-(4RF)	MM-(1)-MP
Daesiidae (excl. *Namibesia*)[c]	FD-(0,1)-FM-(1,2)-FP-(3,4RF)	MM-(0?,1)-MP
Dinorhaxinae Roewer, 1933	FD-(1)-FM-(1)-FP-(4RF)	MM-(1)-MP
Eremobatidae Kraepelin, 1901[d]	FD-(0,1,2,3)-FM-(1,2,3)-FP-(3-5RF)	MM-(1,2)-MP
Galeodidae Sundevall, 1833[e]	FD-(0,1)-FM-(1,2)-FP-(3RF)	MM-(1-4)-MP
Gylippinae Roewer, 1933	FD-FM-(1)-FP-(4RF)	MM-(1)-MP
Karschiidae Kraepelin, 1899[g]	FD-(1,2)-FM-(1,2,3)-FP-(6-8RF)	MM-(2-3)-MP
Lipophaginae Wharton, 1981[f]	FD-(0,1)-FM-(1)-FP	MM-(1)-MP
Melanoblossiinae Roewer, 1933[h]	FD-(1-3)-FM-(1-4)-FP	MM-(1-5?)-MP
Mummuciidae Roewer, 1934[i]	FD-(0,1)-FM-(1,2)-FP	MM-(1-2)-MP
Rhagodidae Pocock, 1897[j]	FD-FM-FP-(5-6RF)	MM-MP
Solpugidae Leach, 1815 (excl. *Solpugiba* Roewer, 1934)[k]	FD-(0,1)-FM-(1,2)-FP-(4RF)	MM-(1-3)-M
Solpugidae (*Solpugiba*)[l]	FD-(1,2,3)-FM-(1,2,3-5)-FP(4RF)	MM-(1)-MP

[a] More secondary teeth uncommon but present in, e.g., *Sedna pirata* Muma, 1971, with FSD tooth, two FSM teeth, up to two MSM teeth (pl. 149D); *Pseudocleobis andinus* (Pocock, 1899) with FSD tooth, up to three MSM teeth (Muma, 1971: 15, fig. 24); *Pseudocleobis chilensis* Roewer, 1934 with FSD tooth, two FSM teeth (Muma, 1971: 19, fig. 31). *Nothopuga* Maury, 1976, partly characterized by absence of FSD and MSM teeth, MSM tooth observed in *N. cuyana* (pls. 146G, H, 147G, H).

[b] See material examined (pls. 132, 133) and Wharton (1981: 40, fig. 35).

[c] FSD teeth rarely present, e.g., in *Hemiblossiola kraepelini* Roewer, 1933, and *Gluvia dorsalis* (Latreille, 1817) as *G. chapmani*; second FSM tooth rarely present, e.g., in *Bitonella roeweri* Lawrence, 1935, and *Blossiola longipalpis* Lawrence, 1935; and MSM teeth rarely absent, e.g., in *Blossiola fimbriata* (Roewer, 1934) (Roewer, 1934: 258, fig. 261h, 353, fig. 256a, 385, fig. 273b; Lawrence, 1935: 73, fig. 2, 78, fig. 5). Fixed (dorsal) finger STF present in some *Blossia* sp. (pl. 147). Most common pattern: FD-FM-(1)-FP; MM-(1)-MP.

[d] FSD teeth absent, FD tooth reduced in *Eremorhax* Roewer, 1934 (pl. 72H); second FSD tooth in other genera, e.g., in *Hemerotrecha marginata* (Kraepelin, 1911) (pl. 82E, F), *Horribates bantai* Muma, 1989 (pl. 70J, 78C); more than two FSD and FSM teeth rare, largely restricted to species of *Hemerotrecha* Banks, 1903, and *Chanbria* Muma, 1951 (vide figures in Muma, 1951). Most common pattern in median series: FD-(1)-FM-(2)-FP. RFA denticles in fondal notch excluded from RF tooth count.

[e] FSD teeth rarely absent, e.g., in *Othoes floweri* Hirst, 1911 (Panouse 1964, 52, fig. 2A, B). Between one, e.g., in *Galeodes* sp. (pl. 62I, J), and four, e.g., in *Galeodes araneoides* (Pallas, 1972) (Birula, 1938: 116, fig. 75a) MSM teeth observed. Number of MSM teeth highly variable intraspecifically, e.g., in *Othoes saharae* Panouse, 1960, with one to three MSM teeth (Panouse, 1964: 65).

[f] FSD teeth absent in *Trichotoma* Lawrence, 1968; single FSD tooth in *Bdellophaga* Wharton, 1981 and *Lipophaga* Purcell, 1903.

[g] Third FSM tooth usually a labile denticle.

[h] Melanoblossiinae includes species that exhibit the multidentate condition or a tendency toward it and, consequently, considerable interspecific variation in secondary teeth. Large numbers of secondary teeth, e.g., in female *Lawrencega longitarsis* Lawrence, 1967, with three FSD teeth, four FSM teeth, and five MSM teeth indicated by Lawrence (1967: 7, fig. 4f).

[i] Second MSM tooth rare (e.g., pl. 26D). See counts in Botero-Trujillo (2014: 322).

[j] Rhagodidae: MM tooth usually small, reportedly absent in some species (e.g., Turk, 1960: 121, fig. 9).

(fig. 18B) represents wear or intrinsic variation, and verifying this may require examination of additional specimens.

Although abnormalities in dentition should not be included in estimates of variation, they are not always readily identifiable, emphasizing the need to examine series of specimens, when available. Abnormalities are often confirmed by other characters. An abnormality in one character in a particular individual (e.g., two flagella on a chelicera) may be accompanied by abnormalities in other characters (e.g., "abnormal tarsal variation," Wharton, 1981: 30). Examples of variation in dentition concentrated in a particular specimen were observed in the present study. For example, when variation was recorded in a series of male *Bdellophaga angulata* (*N* = 53 specimens), the presence/absence of 15 teeth was found to vary, but six of the 15 variable teeth were restricted to a single male.

Patterns of Intraspecific Variation in Dentition

During the present study, examination of materials and review of species diagnoses revealed that intrinsic intraspecific variation in dentition, i.e., excluding wear and deformity, is common in Solifugae. However, this variation, which concerns presence/absence, relative size, and shape, is largely restricted to predictable components of dentition.

The literature suggests that the fondal teeth and the secondary teeth of the median series are more prone to variation than the primary teeth (e.g., Maury, 1976) both within individuals (tables 11) and populations (table 12). A summary of literature references to variation in presence/absence of primary, secondary, and fondal teeth, in seven families, 22 species and at least 319 specimens (638 chelicerae), is provided in table 12. These published findings, including variation in shape and relative sizes not included in the table, were compared with data collected during the present study.

Primary Teeth: The present study confirmed that primary teeth are fairly stable intraspecifically in terms of presence/absence (table 13). Variation in presence/absence of a primary tooth was observed in five chelicerae (one FD tooth in a female *Zeria venator*; two FD teeth and two FM teeth in karschiids, and no variation in FP, MM or MP teeth) or 0.35% (*N* = 310 chelicerae; 20 species; 9 families). This agrees with literature reports; as indicated in table 12, primary teeth were remarkably stable, with no variation in presence/absence recorded. The only taxa in which it was uncertain whether a primary tooth was variable involved the 2–4 "very small apical" teeth of *Blossia sabulosa* (Lawrence, 1972) and the "3–6 small teeth on low ridge adjacent base of flagellum" in *Hexisopus pusillus* Lawrence, 1962, both reported by Wharton (1981: 31, 51). These specimens should be examined to evaluate whether variation exists in the primary or secondary teeth.

In general, the more distally situated in the median series, the more prone teeth appear to vary in presence/absence and relative size. Martins et al. (2004: 2367) reported that an FD

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[k] Single FSD tooth present in few taxa, notably *Solpugista* Roewer, 1934, but also reported in some specimens of, e.g., *Metasolpuga picta* (Kraepelin, 1899) (Wharton, 1981: 67) and *Solpugema aethiops* Lawrence, 1967, based on a single female (Lawrence, 1967: 6, fig. 3a). Three FSM teeth reported only in *Solpuga bovicornis* Lawrence, 1929, the distalmost described as "either low and rounded or else toothlike and resembling the two succeeding teeth and smaller than them" (Lawrence, 1929: 156, fig. 2b, 157). The presence of more than one MSM tooth is rare, with two MSM teeth reported in *Zeriassa purcelli* Hewitt, 1914, based on a single male, the distalmost "being very small" (Hewitt, 1914b: 163, 164, fig. 25), and two MSM teeth not mentioned in original description but illustrated by Roewer (1934: 448, figs. 295b, d) for *Zeria celeripes* (Hirst, 1911) and *Zeria zebrina* (Pocock, 1898), both as *Solpuga* Lichtenstein, 1796. Three MSM teeth were reported in *Solpuga bovicornis*, *Zeria antelopicornis* (Lawrence, 1929), the distalmost described as a "hardly perceptible granule," and *Zeria fusca* (C.L. Koch, 1842) (pls. 116A–D, 117; Lawrence, 1929: 154, 156, fig. 2b; Roewer, 1934: 445, fig. 293a); if three MSM teeth are present, they are situated on distal margin of MP.

[l] Apparently labile denticles are common, especially in later stage juveniles and adults (pl. 110B). The most typical pattern in *Solpugiba* based on juveniles, and ignoring labile denticles, is FD-(1)-FM-(2)-FP.

tooth "may be vestigial" in different specimens of *Mummucia coaraciandu* Pinto-da-Rocha and Rocha, 2004. A specimen of *Gaucha fasciata* Mello-Leitão, 1924 examined during the present study possessed a small tooth, resembling a secondary tooth, distal to two distinct primary teeth (pl. 151A). In a redescription of this species, Maury (1970: 359, 360) mentioned that both anterior teeth were similar in size and this was depicted in figures 2 and 3 (the former reproduced in pl. 151B). The *G. fasciata* example illustrates intraspecific variation in the size of the FD tooth, the distalmost primary tooth. It also confirms that a small tooth, situated distal to the FM tooth and superficially resembling a secondary tooth, is most likely the FD tooth. Even if the specimen illustrated by Maury (1970: 359, 360, figs. 2, 3) proved not to be conspecific with that examined in the present study, the two specimens are closely related, supporting the conclusion that a small FD tooth, rather than an FSD tooth, is the distalmost tooth in these taxa.

Patterns of dentition are generally similar in closely related species and conspecific males and females. Increased variation in distal teeth accounts for variation among closely related species. This was first noted by Maury (1980b: 41), who mentioned that interspecific variation in *Pseudocleobis* was "near exclusively" restricted to the "anterior teeth" on the fixed (dorsal) finger, where the FD, FSD, and FM teeth may be reduced or absent. In Rhagodidae, the FD and MM teeth are reportedly absent in some species (e.g., Turk, 1960: 121, fig. 9) and tend to be minute if present (pls. 56C–H, 57), again demonstrating that interspecific and probably also intraspecific variation, occurs primarily among the distal teeth, and that size is also correlated with variation. Female *Zeriassa furcicornis* Lawrence, 1929 examined in the present study possessed three distinct primary teeth on the fixed finger whereas, in the single male examined, the distalmost tooth was very small, but positionally homologous with the **fixed finger distal (FD) tooth** of the female (cf. pl. 124A–D). If this tooth is interpreted as a small FD tooth, the general pattern of median series dentition in the male of *Z. furcicornis*, i.e., FD-FM-(2)-FP, is identical to that of the female. This observation reinforces the identity of a distal tooth as a primary tooth, despite its superficial similarity to a secondary tooth, and the tendency for more variation distally than proximally in the median series.

The above examples illustrate two practical implications for homology assessment: (1) A small tooth superficially resembling a secondary tooth, situated distal to the FM tooth or the MP tooth is more likely to be a primary tooth (i.e., the FD tooth or the MM tooth, respectively) than a secondary tooth (i.e., the FSM tooth or the MSM tooth, respectively). (2) On the movable (ventral) finger, the medial (MM) tooth is more likely to be absent or variable in size than the proximal (MP) tooth. Similarly, on the fixed (dorsal) finger, a distal (FD) tooth is more likely to be absent or variable in size than a medial (FM) tooth, which, in turn, is more likely to be absent or variable in size than a proximal (FP) tooth.

Exceptions to the apparently greater stability of primary teeth relative to secondary teeth include cases in which a medial (FM or MM) tooth is absent and a submedial (FSM and MSM) tooth present, the latter situated very close to a proximal (FP or MP) tooth, often on the distal margin of the proximal tooth itself. Examples on the movable finger occur in Eremobatidae (e.g., pl. 78B) and on the fixed finger in Gylippinae (e.g., pls. 85B, 86B). The pattern may also be present in Daesiidae (e.g., Roewer, 1934: 398, fig. 278a), but requires further investigation. The identity of the secondary tooth is confirmed in these examples by the simultaneous presence, vestigial or well developed, of the primary tooth in some species (i.e., vestigial FD and FM teeth in Gylippinae and MM tooth in Eremobatidae, respectively). These examples also indicate greater stability among secondary teeth for those situated proximally in the median series, and close to the proximal (FP or MP) tooth.

TABLE 11

Bilateral asymmetry in cheliceral dentition (secondary and fondal teeth) of Solifugae

Abbreviations: **FSM**, fixed finger, submedial tooth/teeth; **MSM**, movable finger, submedial tooth/teeth; **PF**, profondal teeth; **RF**, retrofondal teeth.

Family	Species	Sex	Sinistral	Dextral	References
Ceromidae Roewer, 1933	*Ceroma inerme* Purcell, 1899	♂	1MSM	2MSM[a]	Purcell (1899)
Daesiidae Kraepelin, 1899	*Neocleobis solitarius* (Banks, 1902)	♂	1MSM	2MSM[a]	Muma (1970b)
Galeodidae Sundevall, 1833	*Galeodes afghanus* Pocock, 1895	♂	2MSM	3MSM[b]	Pocock (1895)
	Galeodes bactrianus Birula, 1937	♀	1MSM	2MSM	Birula (1937a)
	Galeodes lycaonis Turk, 1960[c]	♀	2FSM	3FSM[a]	Turk (1960)
	Galeodopsis strandi (Birula 1936)	♂	1MSM	2MSM[a]	Birula (1936a)
Solpugidae Leach, 1815	*Zeria fordi* (Hirst, 1907)	♂	1MSM	2MSM	Simonetta and Delle Cave (1968)
	Zeriassa pardii Simonetta and Delle Cave, 1968[c]	♂	2RF	3RF[d]	Simonetta and Delle Cave (1968)

[a] Additional tooth indicated as "very small" or "minute" (Purcell, 1899: 399).

[b] If absent, space of third tooth left open.

[c] Holotype.

[d] $N = 8$; asymmetry in six specimens; two specimens with three retrofondal (RF) teeth on both chelicerae.

Secondary Teeth: Based on a survey of the literature (table 12), variation in the number of MSM teeth was observed in three species (13.6%; $N = 22$ spp.), in the number of FSM teeth in seven species (31.8%), and in the number of FSD teeth in, at most, six species (27.3%). The present study also confirmed that secondary teeth, especially denticle-sized teeth, are more variable than primary teeth (e.g., figs. 19, 20; table 13). Intraspecific variation in the presence/absence of MSM teeth was observed in 33 chelicerae (11%; $N = 290$ chelicerae), of FSM teeth in 37 chelicerae (15%; $N = 253$), and of FSD teeth in 13 chelicerae (10%; $N = 132$).

Unlike primary teeth that, in general, become more stable proximally (see section on Primary Teeth), based on the literature and material examined, the stability of individual secondary teeth is associated with the direction of size gradation. When two or more teeth are present within categories of secondary (i.e., MSM, FSM and FSD) teeth, a gradation in size is observed, such that the teeth increase in size proximally or distally (table 8). The distalmost teeth are less likely to vary if the teeth increase in size distally, whereas the proximalmost teeth are less likely to vary if the teeth increase in size proximally. Smaller teeth are more likely to vary than larger teeth. Denticles interspersed among larger secondary teeth are the most labile in presence/absence and size (e.g., figs. 19, 20), rarely conforming to patterns of size gradation.

Another pattern observed in the secondary teeth is that the FSD row rarely comprises more teeth than the FSM row (fig. 17C), in accordance with the pattern that more teeth are absent distally than proximally on the fixed finger.

Exceptions to the patterns identified in the present study are rare and usually caused by the presence of tiny denticles. For example, the absence or presence of denticles may result in more FSD teeth than FSM teeth, and the absence of a distinct gradation in size. Although taxa in various families may deviate from general patterns, e.g., *Namibesia pallida* in Daesiidae and *Solpugiba lineata* in Solpugidae, most examples concern species of Eremobatidae. A female of *Horribates bantai* (pl. 78C) possessed three FSD teeth and only two FSM teeth, and size gradation within the FSD row was confounded by a small denticle between two larger FSD teeth. A small denticle situated distally in

TABLE 12

Variation in tooth counts among Solifugae based on the literature

Only teeth that could be unambiguously identified included in assessment. Studies that based species identifications on "number of intermediate [secondary] teeth" were omitted to avoid circular reasoning. Terminology was retrospectively assigned based on descriptions and figures provided by authors, and adapted to fit interpretations in the present contribution. Sources: Hewitt (1914a), Birula (1936b, 1937a), Muma (1951), Simonetta and Delle Cave (1968), Wharton (1981), Maury (1982), Carvalho et al. (2010), González Reyes and Corronca (2013), Botero-Trujillo (2014).

Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth/teeth; **FSM,** fixed finger, submedial tooth/teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth/teeth; **PF,** profondal teeth; **RF,** retrofondal teeth.

Taxon	*N*	FD	FSD	FM	FSM	FP	MM	MSM	MP	RF	PF
Ammotrechidae Roewer, 1934											
Ammotrechella geniculata (C.L. Koch, 1842)	♂	1	0	1	1	1	1	1	1	4	4
	♀	1	0	1	1	1	1	1	1	5	4
Daesiidae Kraepelin, 1899											
Biton (*Biton*) *rossicus* (Birula, 1905)[a]	11 ♂	1	0	1	1	1	1	1	1	?	3–4
Biton (*Bitonissus*) *schelkovnikovi* (Birula, 1938)	5 ♂	1	0	1	1	1	1	1	1	?	3
Blossia planicursor Wharton, 1981	9 ♂	1	0	1	1	1	1	1	1	3	3
Blossia purpurea Wharton, 1981	12 ♂	1	0	1	1	1	1	1	1	3	3
Blossia rooica Wharton, 1981	5 ♂	1	0	1	1	1	1	1	1	3	3
Namibesia pallida Lawrence, 1962[b]	11 ♂	1		1		1	1	1	1	4–5	2–5
Eremobatidae Kraepelin, 1901											
Eremochelis bilobatus (Muma, 1951)[c]	12 ♂	-	-	-	-	-	1	1–2	1	?	?
Galeodidae Sundevall, 1833											
Galeodes setulosus Birula, 1937	♂?	1	0	1	2	1	1	3–4	1	?	?
	9 ♀	1	0	1	2	1	1	3	1	?	?
	7 ♀	1	0	1	2	1	1	2–3	1	?	?
Lipophaginae Wharton, 1981											
Trichotoma fusca (Roewer, 1941)	4 ♂	1	1	1	1–2	1	1	1?	1	5–6	?
Trichotoma michaelseni (Kraepelin, 1914)[d]	4 ♂	1	0	1	0–1	1	1	1	1	6–8	?
	6 ♀	1	0	1	0–1	1	1	1	1	5–6	?
Mummuciidae Roewer, 1934											
Mummucia ibirapemussu Carvalho et al., 2010	16 ♂	1	0	1	1	1	1	1	1	5	3
	3 ♀	1	0	1	1	1	1	1	1	5	2–3
Mummucina puna González Reyes and Corronca, 2013	18 ♂, 4 ♀, 1 juv.	1	1	1	1	1	1	1	1	4–7	3
Mummucina titschaki Roewer, 1934	61 ♂	1	0–1	1	1–2	1	1	1–2	1	5–7	2–4
	8 ♀	1	1–2	1	2	1	1	1–2	1	6–7	3

Taxon	*N*	FD	FSD	FM	FSM	FP	MM	MSM	MP	RF	PF
Solpugidae Leach, 1815											
Metasolpuga picta (Kraepelin, 1899)	18 ♀	1	0–?	1	1	1	1	1	1	?	?
Solpugista hastata (Kraepelin, 1899)[e]	4 ♂	1	1	1	1–2	1	1	1	1	4	3
Solpugema genucornis Lawrence, 1935)	13 ♂	1	0	1	0–1	1	1	1	1	?	?
	6 ♀	1	0–1	1	1	1	1	1	1	?	?
Solpugiba lineata (C.L. Koch, 1842)	?	1	1–3	1	2–4	1	1	1	1	?	?
Solpugista bicolor (Lawrence, 1953)	12 ♀	1	1	1	2	1	1	1	1	?	?
	21 ♂	1	0–1	1	1–2	1	1	1	1	?	?
Zeriassa lepida Kraepelin, 1913	9 ♂	1	0	1	1	1	1	1	1	3	2
Zeriassa pardii Simonetta and Delle Cave, 1914	8 ♂	1	0	1	2	1	1	1	1	2–3	2
Zeriassa ruspolii (Pavesi, 1897)	12 ♂, 6 ♀	1	0	1	2	1	1	1	1	?	?

[a] As *Daesia rossica* Birula, 1905.

[b] Three to six secondary teeth in FSD plus FSM rows.

[c] As *Therobates bilobatus* Muma, 1951.

[d] Second retrofondal tooth large and "followed by cluster or 3–4 small teeth" (Wharton, 1981: 43).

[e] As *Solpuga ornithorhyncha* Hewitt, 1914.

the FSD row results in three FSD teeth and two FSM teeth in the female paratype of *Hemerotrecha hanfordana* Brookhart and Cushing, 2008 (pl. 82D). Other examples include illustrations by Muma (1951) pertaining to species, mostly of *Hemerotrecha*, with more FSD teeth than FSM teeth. These include a male *H. denticulata* Muma, 1951 with no FSM teeth and one FSD tooth (Muma, 1951: 103, fig. 211), females of *H. banksi* Muma, 1951, *H. californica* (Banks, 1899), and *Eremochelis insignatus* Roewer, 1934, each with one FSM tooth and two FSD teeth (Muma, 1951: 97, fig. 191; 101, fig. 195; 109, fig. 221), and a female *H. marginata* (Kraepelin, 1911) with three FSM teeth and four FSD teeth (Muma, 1951: 101, fig. 200). In these examples, the additional secondary teeth that violate general patterns are almost always minute (denticle-sized) and thus probably very labile (e.g., fig. 20). Expected patterns of size gradation, both within and among categories of secondary teeth, are usually obtained when these labile denticles are ignored. It should also be noted that the two denticle-sized FSD teeth of *H. marginata*, illustrated in Muma's (1951: 101) figure 200, which was redrawn from Roewer's (1934: 568) figure 327c, are absent in the female syntype (ZMUH [R8376]; pls. 82F, 83B; also see Brookhart and Cushing, 2008: 57, fig. 29), reiterating how illustrations can be misleading.

FONDAL TEETH: Fondal teeth have been reported to vary considerably in number and size. According to the literature (table 12), variation in the number of profondal (PF) teeth was found in four species (18.2%; *N* = 22 species) and in the number of retrofondal (RF) teeth in six species (27.3%). In the present study, intraspecific variation in the presence/absence of fondal teeth was as follows: RFA (18%; *N* = 136 chelicerae), RFM (0.3%; *N* = 304), RFSM (1.9%; *N* = 208), RFP (0.3%; *N* = 302), RFSP (8.5%; *N* = 259), PFM (2.2%; *N* =139), PFSM (11%; *N* =81), PFP (0.8%; *N* =121), PFSP (3%; *N* =97). Variation was thus more common in particular teeth, the most stable being the RFM and RFP teeth in the retrolateral row, and the PFM and PFP teeth in the profondal row. Examination of individuals within series revealed patterns not only in the number of fondal teeth, but also in their shape and, often, relative size. For example, among males of the lipophagine, *Bdellophaga angulata* (*N* = 53; 106 chelicerae), five teeth were counted in the retrofondal (RF) row of most specimens, each of which was individually recognizable based on its relative posi-

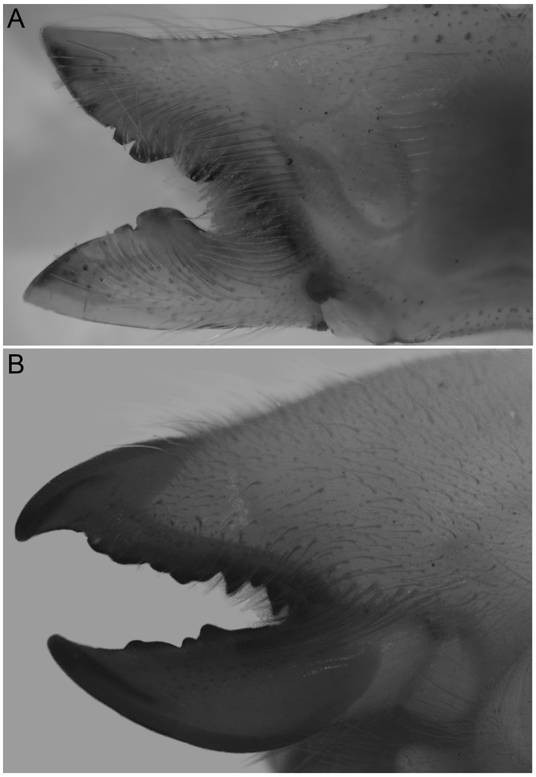

FIG. 18. Solpugidae Leach, 1815, Solpuginae (**A**) and Ferrandiinae Roewer, 1933 (**B**), chelicerae, prolateral (**A**) and retrolateral (**B**) views, illustrating examples of unambiguously deformed or excessively worn dentition (**A**) and seemingly deformed or worn dentition (**B**). **A.** *Solpugella asiatica* Roewer, 1933, ♀ (HUJI). **B.** *Ferrandia robusta* Lawrence, 1954, ♀ (MCZ 126329).

tion, size, and shape, corresponding to the pattern observed in conspecific females. Disregarding three chelicerae with broken teeth, the retrofondal teeth were almost identical in position, size, and shape in all but seven (94%; *N* = 103) chelicerae. Five retrofondal subdistal (RFSD) teeth and two retrofondal subproximal (RFSP) teeth were absent and one retrofondal medial (RFM) tooth was deformed. It is noteworthy that three fondal teeth and three (of five) median series teeth (FSD and FSM teeth) were absent in a single specimen.

A similar example of variation restricted to predictable areas was observed in a series of males of the mummuciid, *Uspallata* cf. *pulchra* (*N* = 26; 52 chelicerae), the homologs of which were each recognizable among individuals. The RFP tooth was readily identifiable in most specimens, but the identity of other teeth in the RF series was less obvious. Based on the structure of individual teeth, the most plausible hypotheses are presented here (pls. 26, 152), with probable homologs numbered one to eight to facilitate discussion (RFA: 1, 2; RFM: 3; RFSM: 4; RFP: 5; RFSP: 6, 7, 8). Two retrofondal subproximal (RFSP) teeth were present in all except six chelicerae (i.e., in 89% of the chelicerae examined), each of which possessed one RFSP tooth instead. A third RFSP tooth was present on one chelicera only (pl. 26B). A retrofondal submedial (RFSM) tooth was present in only five (9%) chelicerae examined (pl. 26D) and the proximalmost retrofondal apical (RFA) tooth, which can be recognized by its curved shape and coloration, resembling teeth of the median series (pl. 26E), was present in all except one (98%). Variation in presence/absence was thus limited and restricted to particular teeth but, in this species, variation in size was more extensive than in *B. angulata.* Such variation in size, together with the previous inability to identify individual teeth, and the difficulty in examining fondal teeth without damaging specimens, may create a false impression that there is no pattern in the fondal teeth of species such as *Uspallata* cf. *pulchra*.

As with primary and secondary teeth, fondal teeth that are usually smaller also tend to be more labile, especially in presence/absence. For example, the most stable profondal teeth are almost always the large profondal proximal (PFP) and profondal medial (PFM) teeth.

INTRASPECIFIC VARIATION IN SHAPE OF TEETH: As with other aspects of solifuge morphology, variation in tooth shape has seldom been evaluated. Kraepelin (1901: 69) used tooth shape as a diagnostic character, but added question marks when uncertain about its stability in particular taxa, e.g., *zweizackigen* (*immer*?) *Hauptzahn*. Examples of tooth shape in species diagnoses and identification keys (Purcell, 1899: 420; Kraepelin, 1901; Turk, 1948: 266; Wharton, 1981: 74) include the fixed finger distal (FD) and medial (FM) teeth “strongly hooked” apically in *Solpugema vincta* (C.L. Koch, 1842); a bifid fixed finger proximal (FP) tooth in *Zeria schweinfurthi* (Karsch, 1880); and the FD, FM, and FP teeth recurved at the apex in the female of *Gylippus shulowi* Turk, 1948. These examples were often based on single specimens, but examination of more material suggests that shape may be relatively stable. Wharton (1981: 63) mentioned the distinct bifurcate movable finger medial (MM) tooth as a diagnostic character of *Solpugista hastata*. Brookhart and Cushing (2004: 286) examined many specimens, and found that the shape of the MM tooth of males, and the presence or absence of a small notch (“cleft”) distal to the MM tooth in both sexes, could be used to diagnose species in the *scaber* group of *Eremobates*. Roewer (1934: 433, fig. 289c_1) noted the presence of a rounded, bifid FP tooth in seven males of *Zeria boehmi* (Kraepelin, 1899).

Even subtle shapes appear to be more consistent than generally recognized. For example, the slightly recurved tips of otherwise symmetric primary teeth were invariant in all male *Uspallata* cf. *pulchra* examined in the present study (*N* = 26; 52 chelicerae) (pl. 152) and similar in shape to the primary teeth of a potentially close relative, *Mummucia coaraciandu* (vide Martins et al., 2004: 2365, fig. 3A, B). The vestigial FST, FD and FM teeth of all male *Melanoblossia braunsi* examined in the present study (*N* = 5; 10 chelicerae) were “folded” in shape (fig. 21; pl. 155E), resembling the same teeth of an undescribed species of *Melanoblossia* (pl. 156A), and those illustrated for *Melanoblossia globiceps* Purcell, 1903 by Wharton (1981: 53, fig. 54). In male *Bdellophaga angulata* examined (*N* = 53; 106 chelicerae), the ventrodistally directed bifid shape, created by partial fusion of the narrow fixed finger distal (FD) tooth to the fixed finger subdistal (FSD) tooth (pls. 87H, 89C), was identical in all except one chelicera (*N* = 49; 98 chelicerae), in which both teeth were present (the FD and FSD teeth of six chelicerae were broken and of two, intensely worn, preventing the evalu-

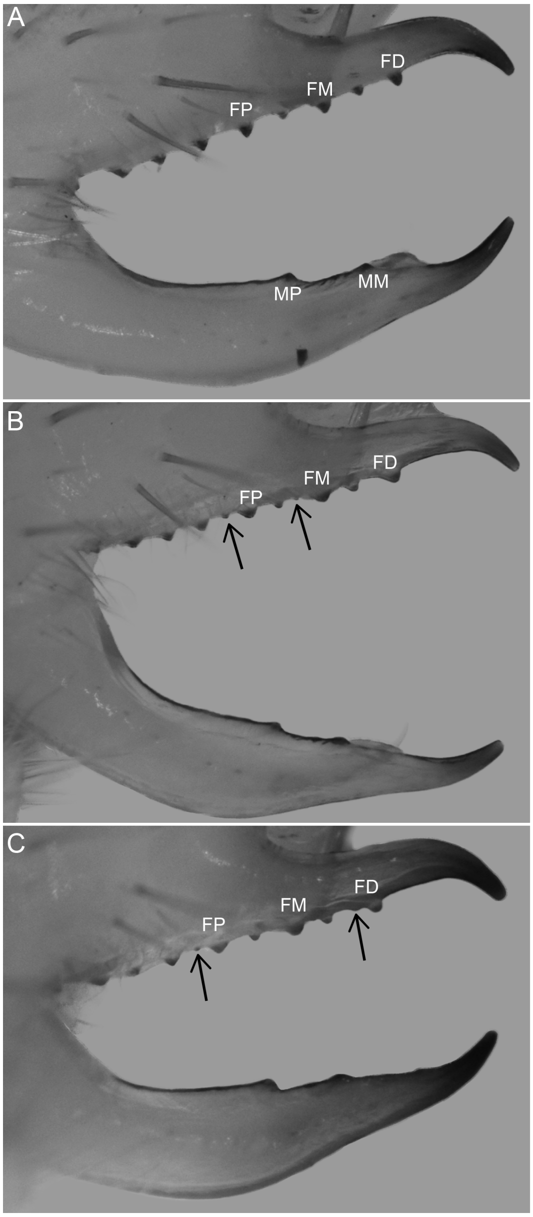

FIG. 19. Karschiidae Kraepelin, 1899, *Eusimonia divina* Birula, 1935, ♂♂ (AMNH [LP 4098]), chelicerae, retrolateral views, indicating intrapopulation variation. Arrows indicate variable teeth (labile denticles). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth.

TABLE 13

Variation in dentition among a sample of Solifugae

Only variable teeth are indicated (FP, MP, and MM teeth were invariant and therefore omitted), and reported as number of chelicerae in which observed out of total number of chelicerae examined (*N*). Numbers in parentheses indicate number of chelicerae in which teeth could be verified, where this differed from *N*. Variation in RFA teeth (from one to three) combined into single count. "n.a." denotes teeth absent in sample, and probably inapplicable to the species; questionmark indicates teeth not verified, e.g., proventral fondal teeth and RFA denticles in fond of male eremobatids. Consult appendix 2 for material examined. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth/teeth; **FSM,** fixed finger, submedial tooth/teeth; **imm.,** immature; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth/teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth/teeth; **RFA,** retrofondal apical tooth/teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth/teeth; **RFSP,** retrofondal subproximal tooth/teeth.

Taxon	♂, ♀	*N*	MSM	FD	FSD	FM	FSM	RFA	RFM	RFSM	RFP	RFSP1	RFSP2	PFM	PFSM	PFP	PFSP
Ceromidae Roewer, 1933																	
Ceroma inerme Purcell, 1899	7 ♂	14	7		n.a.			n.a.		n.a.	1	2	3		n.a.		
Daesiidae Kraepelin, 1899																	
Gluviopsilla discolor (Kraepelin, 1899)	10 ♂	20			n.a.			n.a.					n.a.				
	6 ♀	12			n.a.			n.a.					n.a.				
Eremobatidae Kraepelin, 1901																	
Chanbria regalis Muma, 1951	2 ♀	4						2		1 (2)		1	n.a.	?	?	?	?
Eremobates corpink Brookhart and Cushing, 2004	2 ♂	4			n.a.	n.a.	n.a.		?	?	?	?	?	?	?	?	?
	3 ♀	6						n.a.						?	?	?	?
Eremochelis insignatus Roewer, 1934	5 ♂	10						n.a.	?	?	?	?	?	?	?	?	?
Hemerotrecha branchi Muma, 1951	2 ♂	4	1		n.a.		n.a.	?		n.a.			n.a.	?	?	?	?
Galeodidae Sundevall, 1833																	
Galeodes turkestana Kraepelin, 1899	6 ♂	12	2				3	n.a.		n.a.		2	n.a.	?	?	?	?
	11 ♀	22	6				7	n.a.		n.a.		2 (21)	n.a.	?	?	?	?
	7 imm.	14					1	n.a.		n.a.		5	n.a.	?	?	?	?
Karschiidae Kraepelin, 1899																	
Eusimonia divina Birula, 1935	3 ♂	6	?					1		n.a.			n.a.	2 (12)	n.a.		n.a.
	8 ♀	16		1	2	1	3	8		n.a.		2	n.a.	2	n.a.		n.a.
Karschia (*K.*) *mastigofera* Birula, 1890	2 ♀	4			2								n.a.		n.a.		
Karschia (*K.*) *tibetana* Hirst, 1907	1 ♂	2	1	1			1	1		n.a.			n.a.	?	?	?	?

Taxon	♂, ♀	*N*	MSM	FD	FSD	FM	FSM	RFA	RFM	RFSM	RFP	RFSP1	RFSP2	PFM	PFSM	PFP	PFSP
Lipophaginae Wharton, 1981																	
Bdellophaga angulata Wharton, 1981	53 ♂	104			2		4	5				1	1	?	?	?	?
Trichotoma michaelseni (Kraepelin, 1914)	12 ♂	24			n.a.			n.a.				n.a.	n.a.		5		2
	1 ♀	2			n.a.			n.a.				n.a.	n.a.		1		
Melanoblossiinae Roewer, 1933																	
Melanoblossia sp.	12 ♂	24	11			12		n.a.		1 (19)			n.a.	?	?	?	?
Rhagodidae Pocock, 1897																	
Rhagodes sp.	6 ♂	14	n.a.				n.a.	2		2		n.a.	n.a.	n.a.	?	?	?
	1 ♀	2	n.a.				n.a.					n.a.	n.a.	n.a.	?	?	?
Solpugidae Leach, 1815																	
Oparba asiatica (Turk, 1948)	3 ♂	6						n.a.				1	n.a.		n.a.		
Solpugiba lineata (C.L. Koch, 1842)	13 imm.	26			7		5	n.a.					n.a.		n.a.		
Solpuguna collinata (Purcell, 1903)	4 ♂	8					2	n.a.					n.a.		1		1
Solpugyla sp.	5 ♂	10					4	n.a.					n.a.	1 (2)	1 (2)	1 (2)	1 (2)
	3 ♀	6						n.a.					n.a.	?	?	?	?
Solpugyla cf. *orangica*	2 ♂	4						n.a.					n.a.				
	1 ♀	2					1	n.a.					n.a.				1
Zeria venator (Pocock, 1897)	3 ♂	6						n.a.				2	n.a.		1 (5)		
	1 ♀	2		1				n.a.					n.a.	?	?	?	?

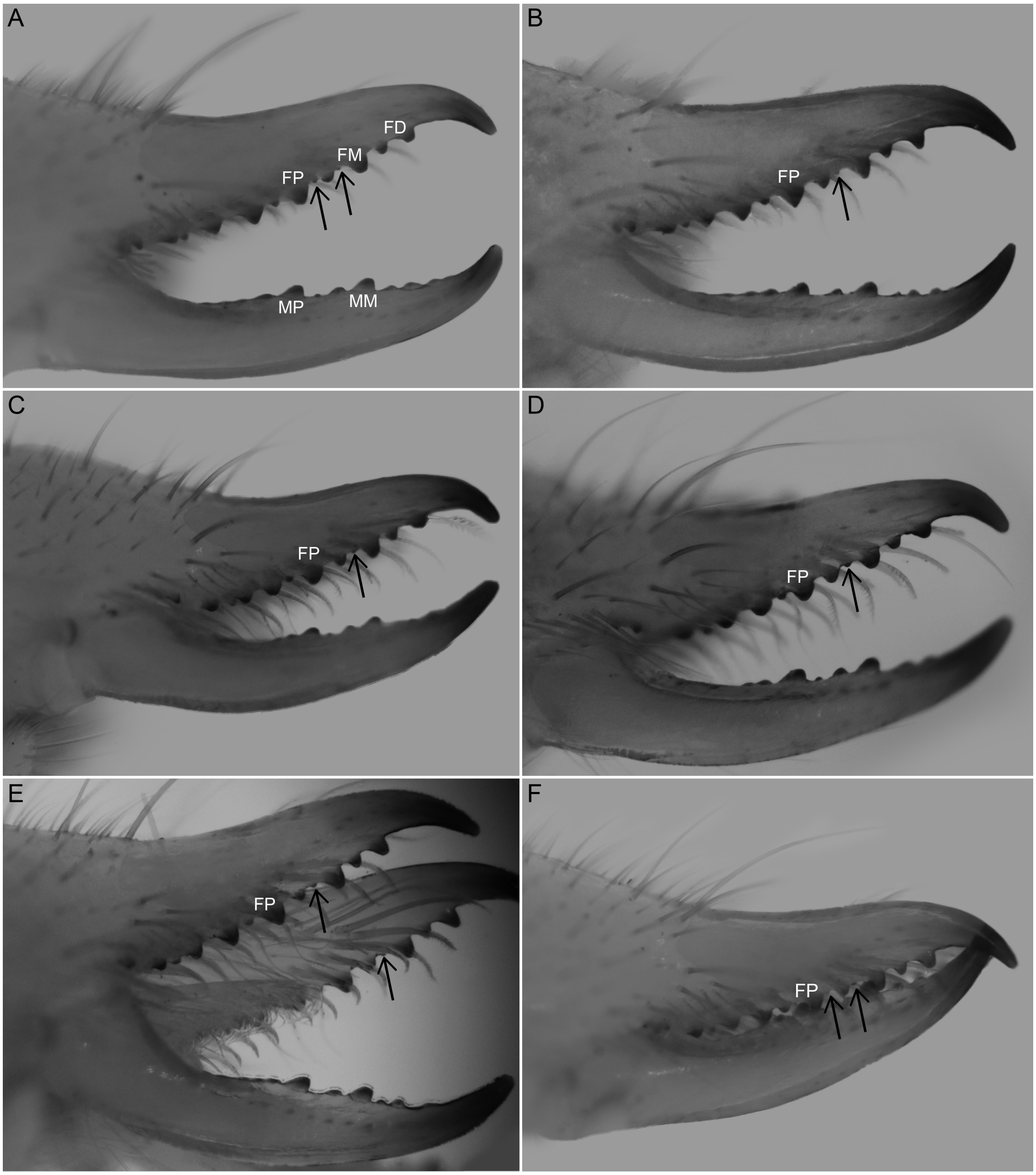

FIG. 20. Karschiidae Kraepelin, 1899, *Eusimonia divina* Birula, 1935, ♀♀ (AMNH [LP 4098]), chelicerae, retrolateral views, indicating intrapopulation variation. Arrows indicate variable teeth (labile denticles). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth.

ation of shape). Distinct, rounded bifid FP and FM teeth were observed in the holotype of *Oparba asiatica* and in two other potentially conspecific males from different localities (pl. 27), as well as in a male *Solpugema brachyceras* (pl. 20H). Although prominent, this shape was not previously noted in either species, perhaps because it was misinterpreted as a worn or aberrant tooth, e.g., cf. plate 27A with Turk's (1948: 270) figure 4 of the same specimen. The systematic value of shape, at least for the primary teeth, remains poorly understood, but should not be dismissed a priori. As the above-mentioned examples illustrate, shape may prove informative for phylogenetic reconstruction or taxon diagnosis at the species level or above, but current understanding of solifuge relationships prevents further assessment.

Criteria for Primary Homology Assessment of Dentition

Objective, explicitly defined criteria for the identification of homologous dentition in solifuges are nonexistent. Criteria for identifying homologous primary, secondary, and fondal teeth are therefore proposed here based on findings described in the section on Patterns of Intraspecific Variation in Dentition. Some problematic cases are also discussed.

Structural and Positional Homology of Primary Teeth: In the present study, four criteria were developed and applied for the identification of homologous primary teeth. The first and second criteria are traditionally used in the solifuge literature but have not been formally stated. The third and fourth criteria were newly developed, based on synthesis of the literature and examination of material representing taxa across the order. These criteria were developed and are discussed here based on unmodified patterns of dentition (pl. 22B), and then extrapolated to modified patterns. Reciprocal illumination (Hennig, 1966) of these criteria was essential to formulate hypotheses of homology for individual teeth in modified patterns of dentition. A summary of the criteria is provided in table 7.

Criterion 1 distinguishes primary teeth from secondary teeth on the basis of structure (size and sclerotization). In the conserved dentition of most females and immatures, primary teeth are easily distinguished from secondary teeth as the largest, sometimes most sclerotized teeth on the fingers, or at least within the median series (pl. 21). There are three primary teeth on the fixed finger and two on the movable finger. When dentition is reduced, modified, or homogeneous, however, it may be difficult to separate primary from secondary teeth, resulting in primary teeth being ignored in descriptions, or potentially miscoded as absent or as secondary teeth in character matrices. For example, the primary teeth of female Karschiidae identified by Roewer (1934: 296, fig. 223; reproduced in pl. 28 with the interpretation presented here color coded for comparison), apparently on the basis of structural criteria, are unlikely to be homologous. Two corollaries of criterion 1 are therefore proposed to prevent reduced primary teeth from being mistaken for secondary teeth. These corollaries are justified by observations that primary teeth are more stable than secondary teeth, and that stability increases with proximal position on the finger (see section on Patterns of Intraspecific Variation in Dentition, including tables 12 and 13). These corollaries are supported by observations of similar patterns among conspecifics of the same or different sex, e.g., male *Gaucha fasciata* (pl. 151A, B) and male and female *Zeriassa* (pl. 124B, D), and among related species, e.g., *Zeriassa furcicornis* (pl. 124B) and other solpugid genera (e.g., pl. 121H).

Corollary 1 states that secondary teeth are more likely to be absent than primary teeth. Therefore, when a distinct primary tooth is not evident, but a small tooth or denticle is present in the same position, the small tooth or denticle is more parsimoniously assumed to be a reduced primary tooth than a secondary tooth. For example, if one or more teeth are observed distal to the FM tooth then, regardless of size, the distalmost thereof is assumed to be the FD tooth, rather than a secondary tooth.

Corollary 2 states that primary teeth are more likely to be reduced or absent distally on the finger. Consequently, the fixed finger distal (FD) tooth is the first primary tooth to be reduced or absent, the fixed finger proximal (FP) tooth is the last primary tooth to be reduced or absent, the proximal (FP or MP) tooth is usually the largest tooth on a cheliceral finger and, when only two distinct primary teeth are present on the fixed finger, the FD (not FM) tooth is assumed to be absent. There are few examples in which a probable FP tooth is absent while FM and/or FD teeth are present. In the present study, this was recorded in only a few species, mainly belonging to *Hemerotrecha*, with its reduced FP tooth (pls. 79J, 82H, 83C; Brookhart and Cushing, 2002: 94, figs. 32, 33). Corollary 2 is also true among categories of secondary teeth but not within them, i.e., a subdistal (FSD) tooth is more likely to be absent than a submedial (FSM) tooth, but, within a row of FSD teeth, the tooth most likely to be absent is hypothesized to depend on the direction of size gradation within that row, such that the smallest is the most likely to be absent.

Corollary 2 was found to be more applicable, the more proximal a tooth was situated in the median series. This is based largely on examples in which the **movable finger proximal (MP) tooth** and movable finger submedial (MSM) teeth are present, and the movable finger medial (MM) tooth absent (in Eremobatidae, pl. 78B), and a similar pattern on the fixed finger, in which the fixed finger proximal (FP) and fixed finger submedial (FSM) teeth are present and the fixed finger medial (FM) tooth absent (in Gylippinae, pls. 85B, 86B).

Criterion 2 formalizes the intuitive method by means of which the primary teeth have traditionally been named (e.g., Roewer, 1934, 1941; Muma, 1951) based on their positional order on the cheliceral fingers. Three primary teeth are situated on the fixed (dorsal) finger, i.e., the FP, FM, and FD teeth, the FP tooth being the proximalmost primary tooth and often the largest on the finger, followed distally by the FM and FD teeth. Two primary teeth are situated on the movable (ventral) finger, i.e., the MP and MM teeth, the MP tooth being the proximalmost primary tooth on the finger and the MM tooth, the distalmost. Only in rare cases was this arrangement not observed, i.e., the FP tooth was reduced to absent whereas the FM and/or FD teeth were present in some *Hemerotrecha* (pls. 79J, 82H, 83C).

Criterion 3 refers to the pattern by means of which the teeth interlock and/or overlap when the cheliceral fingers are closed, i.e., the relative positions of the teeth on opposite fingers (pl. 29). The articulation of the movable finger with the paturon restricts its movement, in turn constraining the interlock and/or overlap of the dentition to a rigid, fixed pattern. The MP tooth usually fits between the two converging rows of fondal teeth, the FP tooth fits directly distal to the MP tooth, in a space provided by a smaller submedial secondary tooth/teeth, and the FM and FD teeth and any subdistal teeth, if present, fit into the space created by the usually toothless mucron.

The more conserved the dentition (as in pl. 22B), the more precise the interlock of the FP tooth distal to the MP tooth, and the FM tooth distal to the MM tooth, and the less the overlap between the teeth on the fixed and movable fingers. Although the extent of overlap increases with greater modification of the dentition, these patterns of interlock remain, even when the dentition is greatly modified (pl. 29G, I). Closure of the FP tooth proximal to the MP tooth, its putative serial homolog on the movable finger, was not observed in the present study and there are few examples in the literature, e.g., *Biton* (*B.*) *kraekolbei* (Wharton, 1981: 15, fig. 8). Closure of the FP tooth well distal to its homolog on the movable finger is a more common occurrence, e.g., in *Trichotoma michaelseni* (pl. 88E) and an undescribed species of *Melanoblossia* (pl. 156C). In the latter species, the FP tooth even closes distal to the MM tooth (see section on Taxonomic Diversity of Cheliceral Dentition). It should be noted, however, that evaluating patterns of dental overlap from published illustrations, especially those portraying open cheliceral fingers, may be misleading (pl. 29A–C).

Criterion 4 states that similar patterns, e.g., the relative positions, size, and shape of teeth and the presence of other toothlike structures, are observed in conspecifics of the opposite sex and

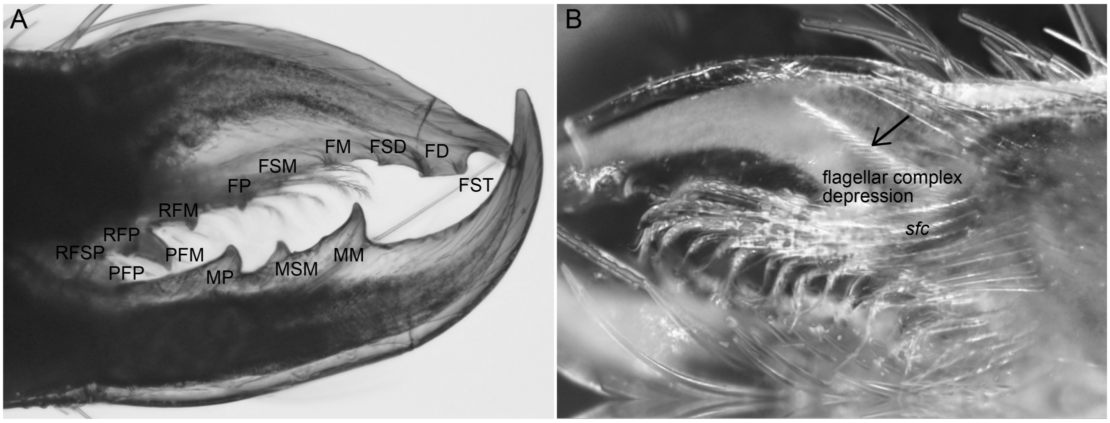

FIG. 21. Melanoblossiinae Roewer, 1933, *Melanoblossia braunsi* Purcell, 1903, ♂ (AMNH [LP 10737]), chelicerae, retrolateral (**A**) and prolateral (**B**) views, indicating hypothesized dentition (**A**) and position of *type C sfc*. Arrow indicates *sfc principal seta*. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **FST,** fixed finger, subterminal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM**, profondal medial tooth; **PFP,** profondal proximal tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth; ***sfc*,** setiform flagellar complex.

in closely related heterospecifics. Examples include the parallel, toothlike flanges on the movable finger of all species of Ceromidae (e.g., pl. 92A) and the "fourth tooth," or **subterminal flange** (**STF**), on the fixed (dorsal) finger of species in the *tricolor* and *setigera* groups of *Blossia* (pls. 144B, D, 145B, D) and toothlike pro- and retrolateral flanges on the movable (ventral) finger of some species in the *setigera* group (e.g., pls. 144E, 145E).

Biton (*B.*) *rossicus* (Birula, 1905) (pls. 136E–H, 138) provides a convenient example of how the aforementioned criteria enable identification of structures with unclear affinities. Individual teeth and toothlike structures are numbered (1–5) to facilitate discussion. In males of this species, the most distinct structures observed on the gnathal edge of the fixed finger in retrolateral view, are a flangelike structure (1) and the three largest teeth (2, 4, 5). Two alternative approaches to naming these teeth are apparent: (1) 5 as the FP tooth, 4 as the FM tooth, 2 as the FD tooth, and an additional toothlike flange distally; or (2) 4 as the FP tooth, 2 as the FM tooth, and the flangelike 1 as a modified FD tooth, leaving 5 as a retrofondal tooth. The extent of sclerotization of the flange, as well as the pattern of dental overlap, suggest that the flange is a primary tooth (FD). This hypothesis is further supported by comparing the modified male dentition with the unmodified conspecific female dentition, which possesses the same number and similar relative sizes of teeth, and with the dentition of related congeners, e.g., *Biton* (*B.*) *browni* (Lawrence, 1963), the dentition of which is similar except for the more distinctly toothlike, and less flangelike, FD tooth (pl. 136I, J).

Single criteria become less reliable as the dentition becomes more markedly modified, requiring greater reliance on reciprocal illumination by multiple criteria. For further examples concerning Ceromidae, *Trichotoma michaelseni* (Lipophaginae), and a species of *Melanoblossia* (Melanoblossiinae), see the section on Taxonomic Diversity of Cheliceral Dentition.

POSITIONAL HOMOLOGY OF SECONDARY TEETH: Hypotheses of primary homology concerning individual secondary teeth are difficult to propose across the order. Unlike primary teeth, there is no fixed number of secondary teeth within a category, e.g., zero (pl. 58) to four (pl. 158) movable finger submedial (MSM) teeth; no obvious

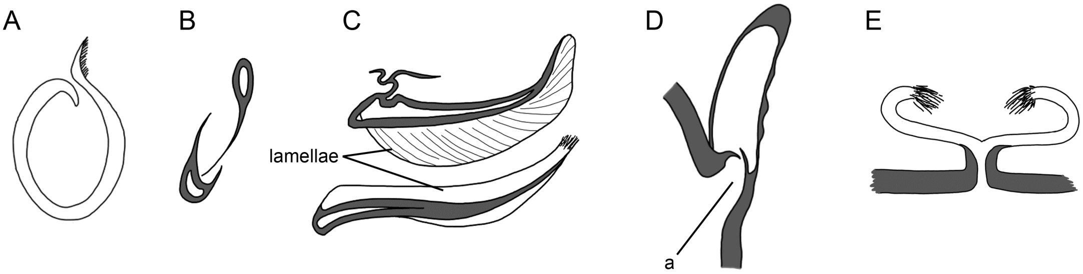

FIG. 22. Karschiidae Kraepelin, 1899 (**A**), Rhagodidae Pocock, 1897 (**B, C**), Solpugidae Leach, 1815 (**D**), and Ammotrechidae Roewer, 1934 (**E**), male flagella, schematic cross sections (**A, B, D, E**) and longitudinal section (**C**), of shaft (**A**), flagellum (**B, C**), bulbous base (**D**) and attachment point (**E**), after Roewer (1934: 138–154, figs. 133c, 137, 143A$_1$, 156). **A.** *Karschia* (*K.*) *tibetana* Hirst, 1907. **B, C.** *Rhagodima nigrocincta* (Bernard, 1893). **D.** *Zeria sericea* (Pocock, 1897). **E.** *Oltacola gomezi* Roewer, 1932. Abbreviation: **a,** atrium.

landmark tooth within a category such as the proximal (FP or MP) teeth on the fixed and movable fingers, respectively; no particular pattern of overlap; and the positions of secondary teeth, relative to the two primary teeth, may vary. Secondary (i.e., FSM, FSD, and MSM) teeth may, however, exhibit a gradation in size (fig. 17A, B; table 8), increasing distally or proximally within a category. Should only one tooth be present within the category, it is assumed to be the tooth at the large end of the size gradation in conspecifics or congeners with more than one tooth in the category. This assumption is supported by observations, e.g., a single MSM tooth is situated closer to the MM tooth in Galeodidae and Karschiidae, in both of which the teeth increase in size distally, but closer to the MP tooth in Eremobatidae and Solpugidae, in both of which the teeth increase in size proximally. A single tooth in a category of secondary teeth is therefore considered homologous in two species if the direction of size gradation of the secondary teeth is the same, i.e., increasing in size proximally or distally, in both species.

Primary homology assessment may be confounded when the direction of size gradation is not obvious, e.g., due to the presence of small teeth, usually denticles, situated between larger secondary teeth. General patterns among secondary teeth are more easily identified when such denticles are treated as labile homologs of other denticles, rather than as vestigial expressions of secondary teeth (which are usually larger), and when comparisons are based on juveniles. When two secondary teeth are present in some conspecifics and absent in others, gaps indicating the positions of absent teeth may imply homology with teeth that are present in other individuals.

Homology of Fondal Teeth: Unlike secondary teeth, several landmark fondal teeth may be identified, i.e., the profondal medial (PFM), profondal proximal (PFP), and (usually) retrofondal proximal (RFP) teeth, on the basis of which other homologs may be inferred. The profondal (PF) row usually possesses at most four teeth including, rarely, a second, small profondal subproximal (PFSP) tooth, of which the PFM and PFP teeth are quite stable, allowing probable homologs to be readily identified in most species. The retrofondal (RF) row is more challenging to homologize, but the RFP tooth constitutes a distinct landmark, based on its shape (equilateral triangular) and position (usually subproximal or proximal in the RF row) in many species (pl. 23), which may be used to identify other homologs, although this is sometimes possible only in conspecifics or congeners.

Supraspecific Patterns of Dentition

Typical patterns of dentition are recurrent above the species level across the order. The pro-

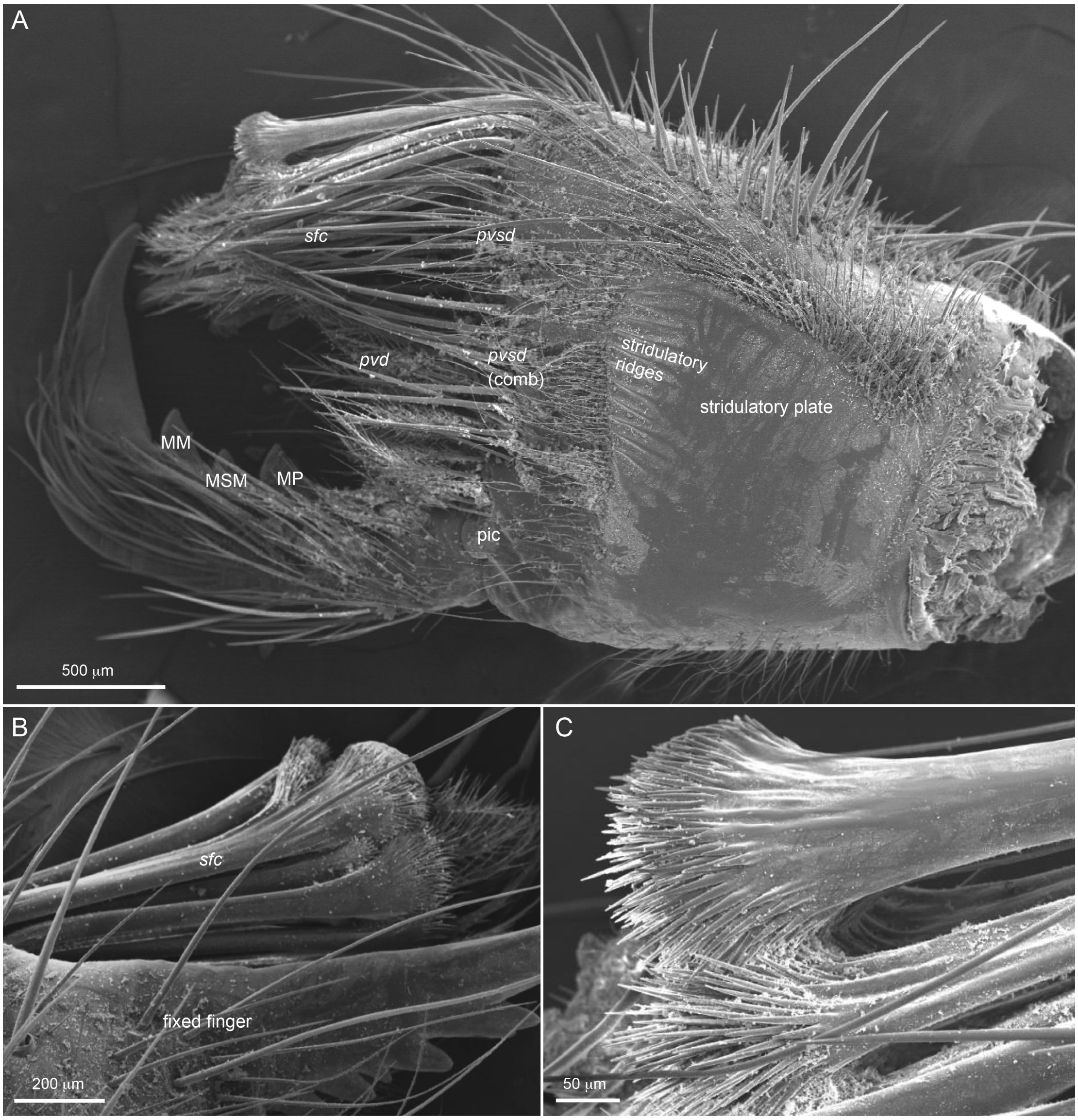
A
sfc
pvsd
pvd
pvsd
(comb)
stridulatory ridges
stridulatory plate
MM
MSM
MP
pic
500 μm
B
sfc
fixed finger
200 μm
C
50 μm

FIG. 23. Lipophaginae Wharton, 1981, *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601), chelicera, prolateral view (**A**) and flagellar complex setae, retrolateral (**B**) and prolateral (**C**) views, indicating stridulatory apparatus and *type B sfc*. Abbreviations: **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **pic,** prolateral interdigital condyle; ***pvd,*** proventral distal setae (plumose); ***pvsd,*** proventral subdistal setae; ***sfc,*** setiform flagellar complex.

fondal medial (PFM) and proximal (PFP) teeth are usually large, tall, and slender whereas the retrofondal proximal (RFP) tooth and, to an extent, the retrofondal medial (RFM) tooth, are shaped like an equilateral triangle. Primary teeth of the fixed (dorsal) finger are often identical in size and shape. For example, all three primary teeth are identical in size and shape in some Mummuciidae (pl. 149G), the fixed finger distal (FD) tooth is identical to the fixed finger medial (FM) tooth in male Ceromidae (pl. 91), and the FM tooth is identical to the fixed finger proximal (FP) tooth in various male Solpugidae (pl. 118D, H). Other structures are restricted to specific taxa. These include two parallel flanges situated distal to the movable finger medial (MM) tooth in male Ceromidae (e.g., pl. 92A); an additional toothlike subterminal flange (STF), situated distal to the FD tooth, in male *Solpugema* (pls. 106E, F, 107A, 109E, F) and males of the *tricolor* group of *Blossia* (pls. 144B, D, 145B, D); or toothlike flanges, situated distal to the MM tooth, in males of the *crepidulifera* group of *Blossia* (e.g., Wharton, 1981: 23, 24, figs. 15, 23), or on the fixed finger and, in some species, on the movable finger in males of the *setigera* group of *Blossia* (e.g., pls. 144E, 145E). These and other similar patterns may represent potential synapomorphies. Furthermore, patterns observed in both sexes and all life stages may enable females and juveniles to be assigned to families, subfamilies, or genera, as in the case of an exceptionally large RFP tooth in both sexes of Lipophaginae, the medial (FM and MM) teeth much larger than other primary teeth in Hexisopodidae, and the FM tooth usually distinctly larger than the FP and FD teeth in *Zeriassa*.

Functional Morphology of Dentition

Sexual Dimorphism, Plesiomorphic Condition, and Feeding: As with other cheliceral characters such as shape, the pronounced sexual dimorphism in solifuge dentition reflects the function of dentition in the sexes (Roewer, 1934: 56; Lawrence, 1965b). The brief lifespan of males, indicated by numerous life history studies and observations (e.g., Heymons, 1902; Amitai et al., 1962; Muma, 1966b; Wharton, 1987), appears to be associated with a reduction in feeding, at least in some species. Whereas some male solifuges feed readily (Cloudsley-Thompson, 1961; Muma, 1966b), others appear to feed rarely, opportunistically, or selectively (Junqua, 1962; Wharton, 1987; Hrušková-Martišová et al., 2010b). The connection between reduced cheliceral dentition in male solifuges (“smaller, blunter and/or less numerous teeth”), a short lifespan with less emphasis on feeding, and adaptation toward mating, was first suggested by Wharton (1987: 372).

Feeding is clearly the primary function of the cheliceral dentition of females. Except for a few termitophagous species, solifuges appear to be generalist predators (e.g., Muma, 1966c; Wharton and Reddick, 2014). Accordingly, there is little pressure for interspecific differentiation of the chelicera except in adult males, in which differentiation is driven by sexual, rather than natural, selection. The number, size, and shape of the dentition of female and, usually, immature solifuges is remarkably uniform interspecifically, and thus probably represents the plesiomorphic condition (Wharton, 1981). According to Wharton (1981), the putative plesiomorphic condition for southern African solifuges (Daesiidae, Hexisopodidae, Lipophaginae, Melanoblossiinae, and Solpugidae) comprises five primary (FD, FM, FP, MM, and MP) teeth, two submedial (FSM and MSM) teeth, and three or four fondal teeth in the PF and RF rows (pl. 22B). Based on the present study, this pattern appears to be conserved in females and immatures across the order. By definition, the plesiomorphic pattern therefore does not include a subdistal (FSD) tooth, which is, however, a relatively common addition to this otherwise conserved pattern. The putatively plesiomorphic dentition of the movable (ventral) finger is also consistent with the fossil record. The enigmatic solifugelike arachnid *Schneidarachne saganii* Dunlop and Rössler, 2003, possesses three teeth on the movable finger (Dunlop and Rössler, 2003: 397, fig. 6).

Although dentition is conserved in most females, there are exceptions, notably the multidentate chelicerae of Karschiidae and Melanoblossiinae. These suprageneric taxa tend to comprise small, microphagous species and the multidentate condition is probably an adaptation to microphagy, involving small, fast running prey. Little or no sexual dimorphism in dentition is evident in the

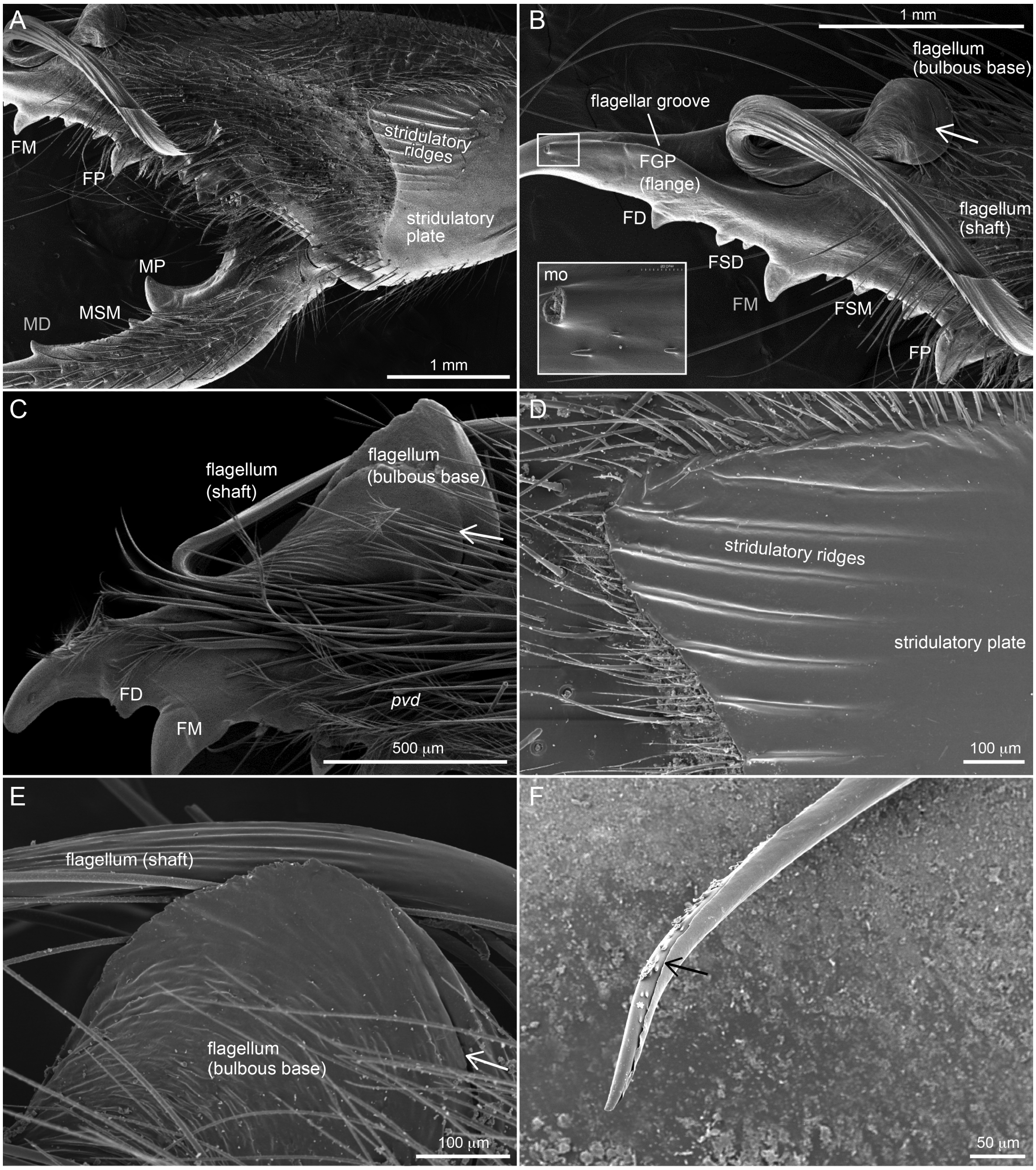
A
FM
FP
MP
MSM
MD
stridulatory ridges
stridulatory plate
1 mm
B
1 mm
flagellum (bulbous base)
flagellar groove
FGP (flange)
FD
FSD
FM
FSM
FP
flagellum (shaft)
mo
C
flagellum (shaft)
flagellum (bulbous base)
FD
FM
pvd
500 μm
D
stridulatory ridges
stridulatory plate
100 μm
E
flagellum (shaft)
flagellum (bulbous base)
100 μm
F
50 μm

FIG. 24. Solpugidae Leach, 1815, chelicerae and cheliceral fixed fingers, prolateral views (**A–D**), indicating stridulatory organs (**A, D**), bulbous base of flagellum, prolateral view (**E**), and apex of flagellar shaft, prolateral view (**F**). **A, B.** *Solpugiba lineata* (C.L. Koch, 1842), ♂ (NMNW 13814), shaft distorted during processing for scanning electron microscopy. Inset: closeup of mucron organ (mo). **C.** *Zeriassa cuneicornis* (Purcell, 1899), ♂ (NMNW 13883). **D, E.** *Zeria sericea* (Pocock, 1897), ♂ (NMNW 13800). **F.** *Metasolpuga picta* (Kraepelin, 1899), ♂, Namibia: Gobabeb. Arrows indicate suture in bulbous base (**B, C, E**) and shaft (**F**). Abbreviations: **FD,** fixed finger, distal tooth; **FGP,** flagellar groove process; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **MD,** movable finger, distal tooth; **MM,** movable finger, medial tooth; **mo,** mucron organ; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pvd*,** proventral distal setae.

larger, termitophagous *Solpugiba lineata* (Solpugidae), in which the dentition of both sexes is slightly reduced in size, with an increased number of secondary teeth, resembling the multidentate condition (pls. 110A–D, 111). Species of *Hemiblossia* (Daesiidae), also known to be termitophagous (Lawrence, 1963; Wharton, 1981), display little sexual dimorphism and, especially in the *australis* group, the primary and secondary teeth are relatively homogeneous in size (pl. 139J), resembling the multidentate condition.

Although reduction in the size and/or number of teeth, and blunting of the terminal teeth in males are usually interpreted as adaptations for sexual reproduction (e.g., Wharton, 1987), slight differences between the sexes might be more parsimoniously explained by reduced feeding in males (Roewer, 1934: 56; Lawrence, 1965b). The diet of males might be limited to less sclerotized prey (Lawrence, 1965b), a hypothesis confirmed by some laboratory observations (Hrušková-Martišová et al., 2010a). A similar argument was advanced above to account for the gracile shape of the male cheliceral manus (see section on Functional Morphology of Chelicerae).

Reproduction: Even when the dentition is similar in both sexes, as in *Solpugiba lineata*, the chelicerae are dimorphic in other respects, e.g., the fingers are longer, the mucra more strongly curved, and the distal (FM, FSD, FD) teeth of the fixed finger more distally directed in the male. Reduced male dentition and more distally directed teeth may reduce injury to the female during violent and forceful chewing of the female prosoma and/or opisthosoma by the male, and/or reduce damage during the genital contact phase, which prepares the female for sperm transfer and often involves vigorous chewing actions of the genital opening and surrounding area by the male (Heymons, 1902; Muma, 1966b). Indeed, opisthosomal kneading was not reported in an ammotrechid, *Oltacola chacoensis*, with pronounced teeth (Peretti and Willemart, 2007), whereas forceful kneading of the female was reported in two galeodids with very blunt teeth (Heymons, 1902; Amitai et al., 1962; Hrušková-Martišová et al., 2008a, 2010a) and a solpugid with small, reduced teeth (Wharton, 1987). Reduced teeth were, however, similarly common in families and species for which light kneading was reported, such as several eremobatids, which are toothless (Muma, 1966b: 347; Punzo, 1998b), a daesiid, *Gluvia dorsalis*, in which the finger is toothless distally but armed with pronounced median teeth proximally (Hrušková-Martišová et al., 2010a), and at least one galeodid with blunt teeth (Cloudsley-Thompson, 1961). Accordingly, there appears to be little correlation between heavy kneading and reduced male dentition, even within genera, hence reduced dentition may not function to reduce injury to females. Forced copulation (coercion) has also been documented in solifuges (Peretti and Willemart, 2007; Hrušková-Martišová et al., 2010a).

There is also no apparent correlation between the development of dentition and the insertion of the fixed finger into the female genital tract during the genital contact phase. For example, the fixed finger is largely toothless in Eremobatidae, where the male “thrusts the needlelike fixed fingers of his chelicera deep into” the female genital tract (Muma, 1966b: 347), whereas teeth are well developed on the fixed finger of Ammotrechidae for which a similar “rapid intromission” of the fixed finger in the female reproductive tract has been reported (Peretti and Willemart, 2007: 33). It may be significant that modification of the fixed finger into an elongated stylet, abruptly constricted from the fondal area, is usually associated with greatly reduced or absent dentition. This morphology, first noted by Kraepelin (1908a), and predominant among Eremobatidae, is also observed in *Biton* (Daesiidae) and *Gylippus* (Gylippinae).

The limited data available do not suggest an obvious connection between reduced male dentition and any aspect of mating, including behavior, which risks injuring females. Alternatively, reduced dentition may limit injury to males during mating. Hrušková-Martišová et al. (2010a: 95, fig. 3) reported that some teeth, including the terminal teeth, of a male daesiid broke off during postinsemination behavior. It should be noted, however, that behavioral observations remain subjective, and descriptions unstandardized across studies, rendering reports of mating behavior largely incomparable.

Although the psammophilous, fossorial adaptations of Hexisopodidae are reflected in their chelicerae, habitat alone is insufficient to explain the modified dentition of males. As both sexes are fossorial and thus subjected to similar selection pressures, the sexual dimorphism of dentition is probably related to reproductive behavior, which may involve encircling the entire body of the female with the greatly curved fixed and movable fingers and reduced dentition, during the somatic copulatory phase (pls. 126–130).

In contrast to the widespread pattern of reduced male dentition, some males possess additional toothlike structures or some exceptionally enlarged, rather than reduced, teeth. Examples of subterminal flanges situated distal to the distal (FD and/or MD) teeth are observed in various species of *Blossia* Simon, 1880 (pl. 144C–F) and *Solpugema* (pl. 109F). Examples of exceptionally large teeth are observed mostly in Daesiidae, and usually restricted to the movable finger, e.g., in *Biton* (*B.*) *truncatidens* (pl. 137C), the FM tooth appears to close into the large, concave MM tooth. Such modifications remain rare, as movable finger dentition is usually rather conserved in male solifuges.

Taxonomic Diversity of Dentition

Ammotrechidae: The typical ammotrechid fixed finger possesses three distinct primary teeth and a single submedial tooth (pls. 23W, X, 24L, M, 25M, 146–148, 149A–D, 150, 153G, H). A subdistal tooth may be absent or present. A movable finger prolateral (MPL) tooth may also be present (e.g., pl. 147E; Muma, 1951; Maury, 1984). As with cheliceral shape, however, sexual dimorphism in ammotrechid dentition varies from weak to strong, depending on the species, and concerns the size and positions of teeth. Examples of such dimorphism include vestigial teeth associ-

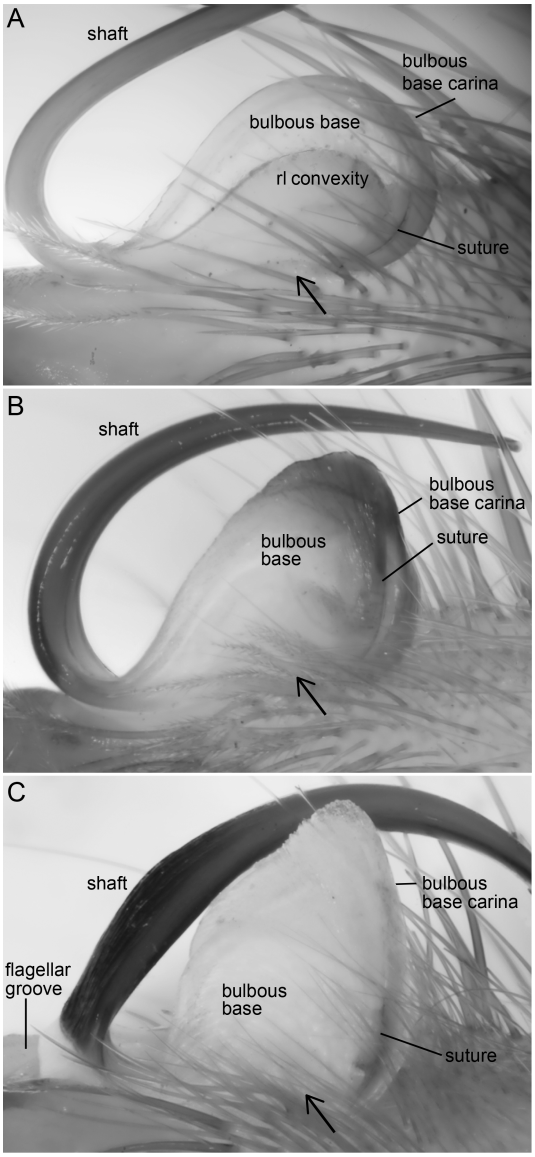

FIG. 25. Solpugidae Leach, 1815, cheliceral flagella, prolateral views, indicating detail of bulbous base with smooth (**A, B**) and jagged (**C**) bulbous base carinae. **A.** *Zeria glabricornis* (Lawrence, 1928), ♂ (AMNH [LP 3614]), retrolateral convexity visible through transparent bulb. **B.** *Solpugyla* sp., ♂ (AMNH [LP 10764]). **C.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). Arrows indicate bulbous base attachment. Abbreviation: **rl,** retrolateral.

ated with a finger that approaches a stylet in shape, e.g., in *Ammotrechula mulaiki* Muma, 1951; a distinct, albeit weakly developed medial notch, e.g., in *Branchia angustus* Muma, 1951; and a proximal shift in the teeth of the median series, e.g., in *Procleobis patagonicus* (Holmberg, 1876) (fig. 7D, pl. 150C; Muma, 1951: 131, figs. 291–292; Muma, 1951: 136, fig. 305).

Ceromidae: The pattern of dentition in Ceromidae is complex (pls. 23O, P, 24D, 25E, 91–96) and highlights the importance of comparison between sexes and among taxa (criterion 4; table 7), inference based on large series, and examination of specimens rather than images. Roewer (1934: 323) recognized the three primary teeth on the fixed finger of male *Ceromella*, an interpretation adopted in the present study (pl. 95), but considered the fixed (dorsal) finger dentition of *Ceroma* to comprise "two anterior teeth" (the FD and FM teeth), situated directly distal to the fondal teeth, implying the absence of secondary teeth (the FSD and FSM teeth) and the proximal (FP) tooth (pl. 92B). Two alternative interpretations of fixed finger dentition are therefore (1) two large, similar, distally situated FP and FM teeth, with the FD tooth absent (pl. 92B) or (2) two large, similar, distally situated FM and FD teeth, with a small, insignificant FP tooth situated proximally (pl. 92C). The more conserved dentition of the female of *Ceroma inerme* (pl. 92D, E) and the related *Ceromella* (pl. 95) supports the second interpretation (pl. 92C, indicated with a check mark) rather than the first (pl. 92B, indicated with an "X"). Absence of a proximal (FP) tooth, together with the presence of medial (FM) and distal (FD) teeth on the fixed finger, contradicts corollary 2 of criterion 1 (table 7), and further supports the second interpretation. Roewer's (1934) interpretation of the dentition of *Ceroma* is therefore dismissed and the second interpretation applied to other ceromid species (pls. 93, 94).

The movable (ventral) finger dentition was fairly conserved in *Ceroma inerme* and the *Ceromella* species examined in the present study. Distinct, movable finger proximal (MP) and medial (MM) teeth are separated by a small submedial (MSM) tooth (pls. 92, 95). A prominent prolateral flangelike carina, described by Purcell (1899: 399) as "inner keel sub-dentiform," parallel to a pronounced, raised, flangelike gnathal edge, is situated distal to the MM tooth. This pair of carinae distal to the MM tooth creates a deep sulcus (Purcell, 1899). The movable finger dentition of *Ceroma swierstrae* Lawrence, 1935 (pls. 91G, H, 94) and, to a greater extent, *Ceroma ornatum* Karsch, 1885 (pls. 91E, F, 93), is more complex, and two interpretations are proposed: (1) an MP tooth and a modified, bicuspid MM tooth, separated by a secondary tooth of similar size, and without a flange distal to the MM tooth (pl. 94E), or (2) MP and MM teeth of similar size, not separated by a secondary tooth, and situated proximal to a toothlike structure comprising a compressed, prolateral flangelike carina parallel to an equally compressed, raised, flangelike gnathal edge (pl. 94B). The first interpretation, according to which the distalmost structure is interpreted as a modified MM tooth rather than as parallel flangelike carinae, is less parsimonious as it implies firstly that the submedial tooth is approximately the same size as the primary tooth, whereas the pattern in other ceromids suggests a greatly reduced secondary tooth, and secondly that the flangelike carinae have either been lost or fused with an MM tooth. The second interpretation, according to which the MP and MM teeth are situated proximal to a flangelike carina, agrees with the more conserved dentition patterns of other ceromids and is therefore adopted here (pl. 94B, indicated with a check mark, rather than pl. 94E, indicated with an "X"). This interpretation implies absence of the submedial (MSM) tooth, consistent with the observation that secondary teeth are more labile. For example, an MSM tooth was recorded on only one chelicera in one of the two *Ceroma inerme* males examined by Purcell (1899: 396, fig. 14). Both Purcell (1899: 396, fig. 14) and Roewer (1934: 324, fig. 238c) illustrated the chelicera of *C. inerme* without an MSM tooth.

The typical ceromid dentition, excluding *Toreus*, the taxonomic affinities of which are

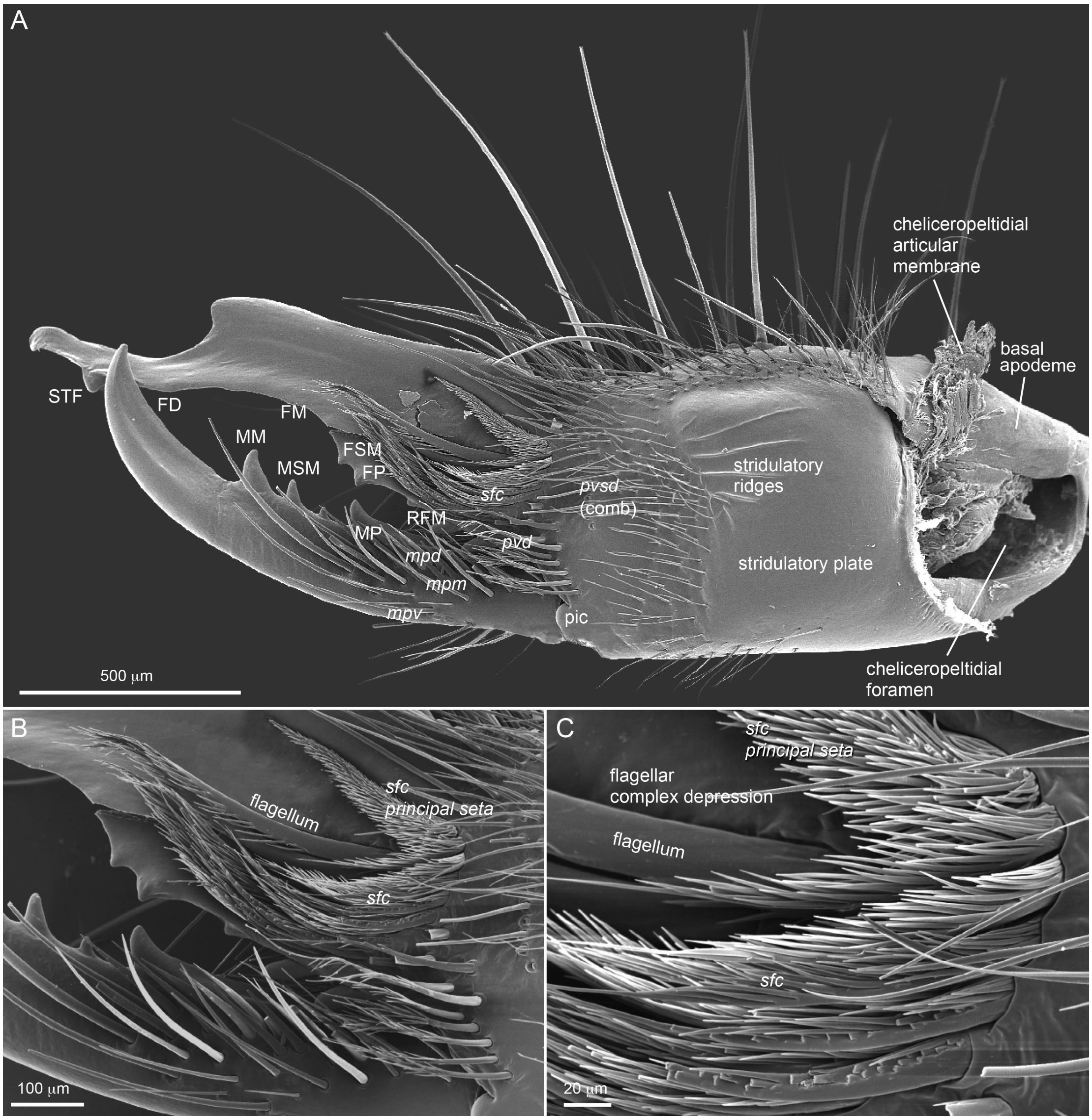
A
cheliceropeltidial articular membrane
basal apodeme
STF
FD
FM
MM
FSM
MSM
FP
sfc
pvsd (comb)
stridulatory ridges
RFM
MP
pvd
mpd
stridulatory plate
mpm
mpv
pic
500 μm
cheliceropeltidial foramen
B
flagellum
sfc principal seta
sfc
100 μm
C
sfc principal seta
flagellar complex depression
flagellum
sfc
20 μm

FIG. 26. Melanoblossiinae Roewer, 1933, *Melanoblossia* sp., ♂ (NMNW 13396), chelicera (**A**) and setiform flagellar complex (**B, C**), prolateral views. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***mpd*,** movable finger prodorsal setae; ***mpm*,** movable finger promedial setae; ***mpv*,** movable finger proventral setae; **MSM,** movable finger, submedial tooth; **pic,** prolateral interdigital condyle; ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae; **RFM,** retrofondal medial tooth; ***sfc*,** setiform flagellar complex; **STF,** subterminal flange.

uncertain (see section on Taxonomic Overview), therefore comprises a relatively small to moderately sized fixed finger proximal (FP) tooth compared to the larger medial (FM) and distal (FD) teeth, which are identical in size and shape. Secondary teeth are often absent on the fixed finger. The movable finger dentition comprises a proximal (MP) tooth and a similar or slightly smaller medial (MM) tooth, sometimes separated by an insignificant, submedial (MSM) tooth (table 10). Distinct parallel, flangelike carinae, situated distal to the MM tooth, one on the prolateral surface and another on the gnathal edge, together forming a sulcus, are characteristic of *Ceroma* and *Ceromella*. The aforementioned interpretations differ from previously published opinions that the tooth, interpreted here as the FP tooth, belongs to the retrofondal (RF) series, and the flangelike carinae on the movable finger represent a modified MM tooth in some species (Purcell, 1899; Roewer, 1934: 323; Wharton, 1981).

The FP tooth of ceromids, especially *Ceroma*, is small in comparison to the rather large FM and FD teeth, an unusual pattern for Solifugae, in which the FP tooth is usually the largest on the fixed finger. The primary teeth are easier to distinguish in *Ceromella*, although they are all relatively small, because the FM and FD teeth are not as enlarged and the difference in size between them and the FP tooth is therefore less pronounced.

There appears to be a transition in the dentition of Ceromidae, from a relatively conserved pattern, with distinct flanges situated distal to the FM tooth, e.g., in *C. inerme*, through an increasingly proximal shift in the flangelike carinae, e.g., in *C. swierstrae*, to a pattern in which the carinae are greatly compressed and situated close to the movable finger median series teeth, superficially resembling a bicuspid tooth instead of parallel, flangelike carinae, e.g., in *C. ornatum*. The proximal shift of the two carinae in *C. ornatum* may be associated with the short chelicera and, particularly, the short movable finger of this species.

Daesiidae: Given the diverse cheliceral morphology of Daesiidae, often involving remarkable modifications (e.g., pl. 137), only the most common, prominent and potentially problematic patterns are discussed here (pls. 23S–V, 24K, 25L, 132I, J, 135–145). Based on a survey of the literature, fixed finger subdistal (FSD) teeth and a second submedial (FSM) tooth are rare in the family, with few exceptions (e.g., pl. 143D, E; table 10). Wharton (1981) questioned the stability of a second FSM tooth in *Biton* (*B.*) *pearsoni* Hewitt, 1914, used by Hewitt (1914a) to distinguish this species from others in the *hottentottus* group.

Hemiblossia, a termitophagous genus, is unusual among Daesiidae due to the limited modification of its dentition, especially in the *australis* group (pl. 139I, J, 141C). Male *Hemiblossia* possess a relatively conserved pattern with pronounced teeth (pls. 139G–J, 141, 142A–D). The medial (FM) and distal (FD) teeth of the fixed finger are similar in shape, and slightly larger than the proximal (FP) tooth in the *bouvieri* group (pl. 139G, H, 141A, B, 142).

Extremely modified chelicerae confound hypotheses of dental homology in two species of Daesiidae. The chelicerae of *Gnosippus klunzingeri* appear to be adapted for burrowing (pls. 136C, D, 137A, B) although the female chelicerae and dentition remain unmodified (Kraepelin, 1901: 100). The teeth of the movable finger are greatly enlarged, the terminal (FT) and distal (FD) teeth of the fixed finger flattened and scooplike, with a cheliceral projection prodorsal to the terminal tooth, referred to by Kraepelin (1908a) as a forked fixed finger. The fixed finger of the unique chelicerae of *Ceratobiton styloceros* is greatly elongated to form a long, slender distal projection, with the FD tooth situated on the projection, approximately aligned with the terminal (MT) tooth of the movable finger (pl. 137D).

Biton is a speciose genus, expressing some of the most highly modified dentition in Solifugae (for examples see Roewer, 1934: 389, figs. 275–279). In some species, the FD tooth is flangelike rather than toothlike (e.g., pls. 136F, J, 143H, I, J). Other notable modifications include an extremely large, modified movable finger medial (MM) tooth, as in *B.* (*B.*) *crassidens* Lawrence, 1935, *B.* (*B.*) *ragazzii* (Kraepelin, 1899), *B.* (*B.*) *simoni* (Kraepelin, 1899) and *B.* (*B.*) *truncatidens* (Kraepelin, 1899: pl. 1, fig. 12a, 13; Lawrence, 1935: 72, fig. 1a; Lawrence, 1954: 115, fig. 3D; Delle Cave and Simonetta, 1971: 50, fig. 4) and a ventrally concave mucron of the fixed finger, with teeth situated on the prolateral margin as in

B. (*B.*) *bellulus* (Pocock, 1902), *B.* (*B.*) *ehrenbergi*, and *B.* (*B.*) *zederbaueri* (see pl. 139B; Kraepelin, 1901: 96, fig. 66; Roewer, 1934: 389, fig. 275c). The primary teeth are often reported as absent in *Biton* (e.g., Roewer, 1934: 389, fig. 275) but should be reexamined as some may be reduced to denticles as noted, e.g., by Lawrence (1962b: 197) in *B.* (*B.*) *tenuifalcis* Lawrence, 1962: "[a]nterior teeth of dorsal jaw absent or represented in front of the first tooth by 2 or 3 obsolete, indistinct granules." In other *Biton* species, only the FD tooth is greatly reduced, as in *Gluvia dorsalis* (pl. 135A).

Among southern African *Blossia*, additional flangelike or small toothlike structures, often characterizing species groups or subgroups (Hewitt, 1919b; Wharton, 1981), are present on the gnathal edges of the mucron distal to the fixed finger distal (FD) tooth and/or the movable finger medial (MM) tooth (pls. 144, 145). Applying the homology criteria for dentition (table 7) suggests that these structures do not belong to any of the usual primary teeth, hence they are termed subterminal flanges (STF), similar to but more toothlike than those on, e.g., the ceromid movable finger mucron.

In the *setifera* group of *Blossia* (e.g., pl. 144E), a flange on the gnathal edge of the movable finger with a prolateral lamelliform carina situated parallel to it ("median lamella" sensu Wharton, 1981: 20), both situated distal to the movable finger medial tooth (MM), resemble an additional bicuspid tooth. This structure has been variously described as a bifid fourth tooth on the movable finger, e.g., in *B. filicornis* Hewitt, 1914, *B. pringlei* (Lamoral, 1974), and *B. setifera* Pocock, 1900 (Pocock, 1900a: 302, fig. 6a; Hewitt, 1914a: 158, fig. 21; Lamoral, 1974: fig. 2); as a fourth "obsolete" tooth "with a transparent lamina on the outer side of the jaw," e.g., in *B. lapidicola* (Lawrence, 1935) (vide Lawrence, 1935: 75, fig. 3); as part of the distal tooth, forming a single trifid tooth, e.g., in *B. falcifera* Kraepelin, 1908 (vide Kraepelin, 1908b); or as a cleft lamella distal to the median series, e.g., in *B. singularis* Lawrence, 1965 (vide Lawrence, 1965a: 56, fig. 3A). Further examples of taxa possessing this structure include *Blossia echinata*, *B. lapidicola*, *B. orangica* (Lawrence, 1935), *B. rooica* Wharton, 1981, *B. singularis*, and various subspecies of *B. falcifera* (pls. 144E, 145E; Purcell, 1903b: pl. 1, fig. 10; Lawrence, 1935: 80, figs. 6, 7, 8; 1965a: 56, fig. 3A).

Additional toothlike subterminal flanges may be present on the fixed or movable fingers, distal to the FD and MM teeth, respectively, in some species of the *crepidulifera* group of *Blossia* (Roewer, 1934: 359; Wharton, 1981). These structures may form a rounded to "taluslike" prominence on the movable finger (Lawrence, 1929: 171). Examples of species possessing this structure include *B. alticursor* Lawrence, 1929, *B. crepidulifera* Purcell, 1902, *B. litoralis*, *B. planicursor* Wharton, 1981, and *B. scapicornis* (Lawrence, 1972) (Purcell, 1902: 215, fig. 4; 1903a: 5, fig. 3; Lawrence, 1929: 171, fig. 14; 1972: 115, fig. 5D; Wharton, 1981: 24, fig. 23). The subterminal flange on the gnathal edge of the fixed finger is usually toothlike. Examples of species that possess this structure include *B. alticursor*, *B. crepidulifera*, and *B. planicursor* (vide Purcell, 1902: 214, fig. 4; Lawrence, 1929: 171, fig. 14; Wharton, 1981: 24, fig. 23). A parallel, prolateral toothlike carina may be situated adjacent to the flange, e.g., in *B. litoralis* (vide Purcell, 1903a: 5, fig. 3).

In the *tricolor* group of *Blossia*, a subterminal flange on the gnathal edge of the fixed finger, resembling a small tooth or tubercle, is present in *B. gaerdesi* (Lawrence, 1972), *B. purpurea* Wharton, 1981, *B. spinicornis* Lawrence, 1928, and *B. tricolor* Hewitt, 1914 (pls. 144B, D, 145B, D; Hewitt, 1914a: 157, fig. 20; Lawrence, 1928: pl. 23, fig. 49; 1972: 114, fig. 4f; Wharton, 1981: 23, fig. 17).

Some *Blossia* species, such as those belonging to the *namaquensis* group and a few others of uncertain affinity (Wharton, 1981), e.g., *B. grandicornis* Lawrence, 1929, do not possess flangelike or toothlike structures in addition to the usual primary teeth (pl. 139D).

Namibesia pallida is unique among Daesiidae in several cheliceral characters, including dentition (pls. 24I, 25J, 132A–D, 133) and was therefore assigned to a monotypic subfamily, Namibesiinae. The movable finger dentition is unmodified in both sexes, with a single movable finger submedial (MSM) tooth situated between pronounced proximal (MP) and medial (MM) teeth. However, an unusually large number of secondary teeth (FSM and FSD) are present on the fixed finger in both sexes. The male and female examined each possessed three fixed finger subdistal (FSD) and one (male) or two (female) fixed finger submedial (FSM) teeth (pl. 133). These counts fall within the range of two or three subdistal (FSD) and submedial (FSM) teeth reported by Maury (1985) for one male and three females; the three subdistal and three submedial teeth reported for *N. purpurea* Lawrence, 1962 (currently in synonymy with *N. pallida*) by Lawrence (1962a: 216), who noted that "one of these intermediate teeth may be extremely small, granuliform or absent, but usually 9 teeth in all;" and the average of four secondary teeth on the fixed finger (*N* = 11 males; range of secondary teeth, 3–6) reported by Wharton (1981: 40, fig. 35).

The male chelicera of *Ammotrechelis goetschi*, another enigmatic, monotypic daesiid species is modified in various respects, but the dentition remains readily identifiable (pls. 24J, 25K, 132E–H, 134). The female dentition of this species is the typical, putatively plesiomorphic pattern with one submedial tooth on both the fixed and movable fingers (FSM tooth and MSM tooth, respectively). The same pattern, although more reduced, is evident in males, which bear distinct proximal (MP) and medial (MM) teeth, separated by a small submedial (MSM) tooth, on the movable finger. The MM tooth is a bicuspid (pl. 134A), parallel and retrolateral to which an additional granular tubercle, referred to here as the **retrolateral granular tubercle**, is situated approximately within the row of granules running retrolaterally along the finger (pl. 134B, D, arrows). Maury's (1985: 5, fig. 3) illustration of a male *Syndaesia mastix* indicates similar structures, i.e., a bicuspid movable finger medial (MM) tooth and a blunt, retrolateral granular tubercle (the *diente pariental* [sic] *externo* of Maury, 1980a: 61, 62), situated retrolateral to the MM tooth, suggesting that *Syndaesia* and *Ammotrechelis* may be closely related. Unfortunately, specimens of *Syndaesia* were unavailable for examination.

Dinorhaxinae: The fixed (dorsal) finger teeth of the male of *Dinorhax rostrumpsittaci* (pls. 23d, 25A, 56A, B, 57A, B) are apically rounded, dome shaped, and more distinctly differentiated than the dentition of the movable finger. The fixed finger proximal (FP) and medial (FM) teeth are readily recognized as primary teeth, but the FD tooth is reduced. The dentition on the movable finger comprises a sharp, jagged gnathal edge, the distinct proximal toothlike structure probably represents the movable finger proximal (MP) tooth, and the vestigial distal tooth, the movable finger medial (MM) tooth. The anterior surface of the MP tooth is notched to form a separate toothlike structure, the position of which resembles the characteristic position of the submedial (MSM) tooth on the movable finger of male Eremobatidae, suggesting that it may be a precursor of the latter. Similarly, denticlelike serrations on the proximal surface of the MP tooth could be precursors of the subproximal (MSP) teeth. The large, jagged MP tooth with a probable MSM tooth on its distal margin is similar to published illustrations (Simon, 1879: pl. 3, fig. 16; Kraepelin, 1901: 41, fig. 12). Differences include a more distinct MM tooth and two additional distinct submedial (MSM) teeth in the published illustrations, which may indicate intraspecific variation. The jagged movable finger gnathal edge and dome-shaped fixed finger teeth are unique among Solifugae.

Eremobatidae: Whereas the dentition of eremobatid males is usually highly modified, with the median series teeth often greatly reduced or absent and the fondal teeth often pronounced, female eremobatids exhibit well-defined dentition patterns, often with additional secondary teeth (pls. 24O, 25P, Q, 65–84). Secondary teeth increase in size proximally within each category (pl. 24O; table 8). Weak basifondal (BF) teeth are present in some taxa (pl.

84C, D, I, J). The retrofondal (RF) row commonly terminates in beadlike retrofondal crenulations on the basal fondal margin. A movable finger prolateral (MPL) tooth is often present, regardless of sex (e.g., pl. 66C).

The typical eremobatid dentition as exemplified by females includes one or two movable finger submedial (MSM) teeth, one fixed finger subdistal (FSD) tooth, two fixed finger submedial (FSM) teeth, and one or two retrofondal apical (RFA) teeth (table 10). The absence of a fixed finger distal (FD) tooth and the presence of "one [intermediate tooth] in front of the medial tooth" were previously suggested as diagnostic characters for the *magnus* group of *Eremorhax* (Muma, 1951: 43). Species with a distinct FD tooth formerly accommodated within *Eremorhax* are currently placed in *Eremocosta* (see Harvey, 2002a) creating the diagnostic character "FD absent" for *Eremorhax* (Brookhart and Brookhart, 2006: 301). As interpreted in the present study, the "intermediate tooth" in question is a reduced distal (FD) tooth, and the diagnostic character is therefore revised to FD tooth reduced, not absent, as in *Eremorhax magnus* (Hancock, 1888) (pl. 72H). Some characters approaching the multidentate condition are often observed in eremobatid females. These include a row of indistinct (e.g., pl. 67D) to pronounced (e.g., pl. 70J) crenulations, referred to as *Sägezänchen* ("saw denticles") by Roewer (1934: 571), situated on the fixed and/or movable finger mucra, proximal to the FP and MP teeth, respectively, and an increased number of secondary (FSD, FSM, and MSM) teeth (Muma, 1951: 39) and retrofondal (RF) teeth.

Reduction or absence of the fixed finger median series, with four large, distinct retrofondal (RFM, RFSM, RFP, and RFSP) teeth is typical of most eremobatid males (fig. 25P). The retrofondal (RF) teeth decrease in size proximally, such that the retrofondal proximal (RFP) tooth is smaller than the RFM and RFSM teeth in many males, especially in *Eremobates* and *Eremochelis* (pl. 78B). Other typical characters are a large movable finger proximal (MP) tooth with a distinct submedial (MSM) tooth distally at the base thereof, and the movable finger medial (MM) tooth almost absent, or modified and flangelike in males (pls. 65, 67, 68). Although the absence of an MM tooth violates corollary 1 of criterion 1 (table 7), the identification of a small submedial (MSM) tooth (not an MM tooth) at the base of the proximal (MP) tooth is supported by examples of congeners bearing distinct MM and MSM teeth, similarly arranged at the base of the MP tooth, e.g., *Eremobates pallipes* (Say, 1823) (pl. 68F). The pattern of dentition in males is corroborated by that in females (pl. 68H). The position of the MSM tooth at the base of the MP tooth or on the margin of the MP tooth itself (e.g., Muma 1951: 68, fig. 95) indicates that it is a secondary tooth rather than a primary tooth. This interpretation of eremobatid dentition agrees with the literature (e.g., Fichter, 1941; Muma, 1951). An additional process, situated distal to the MM tooth on the gnathal edge of the movable finger is evident in some males, e.g., in *Eremochelis imperalis* (Muma, 1951), *Eremocosta gigas* Roewer, 1934, and *Eremocosta striata* (Putnam, 1883) (Muma, 1951: 46, fig. 26; 46, fig. 32; 95, fig. 174, 175).

The retrofondal (RF) teeth of females often appear to include additional retrofondal teeth between the retrofondal medial (RFM) and fixed finger proximal (FP) teeth in females. These are situated on the gnathal edge and often show greater similarity in sclerotization and shape with the median series than the fondal series (e.g., pl. 70). These teeth were referred to as fixed finger subproximal (FSP) teeth by Muma (1951: 47) and Brookhart and Cushing (2004: 285, 286), but are interpreted here as retrofondal apical (RFA) teeth (see section on Dentition Terminology).

Small teeth and denticles are situated in the fondal notch of many eremobatid males (pls. 2B, 4E, 84G, H). These denticles are either ignored in the literature (e.g., Fichter, 1941) or referred to without being assigned to specific categories, e.g., described as "modified teeth in the fondal notch" (Muma, 1951: 61, 108), "aborted teeth of the fixed finger" (Muma, 1951: 108), "supernumerary teeth" (Brookhart and Muma, 1981), or "accessory teeth" (Brookhart and Muma, 1987). According to Muma (1951: 108), Roewer (1934: 570) mistakenly interpreted these denticles as teeth of the retrofondal series. The affinities of the fondal notch denticles remain ambiguous, however. These denticles may be reduced primary teeth that shifted proximally, reduced fondal teeth, subproximal secondary teeth, or additional denticlelike teeth without homologs in females or non-eremobatids. Their identity has implications for the position of the fondal notch relative to particular teeth, and therefore whether the fondal notch of eremobatids is homologous with the medial notch of other taxa (e.g., *Solpugema*). The presence, in some eremobatid males, of highly vestigial, equally spaced primary teeth along the length of the styletlike fixed finger, e.g., in *Eremochelis albaventralis* Brookhart and Cushing, 2005, and *Eremochelis andreasana* (Muma, 1962) (pl. 76C, D), does not support the hypothesis that the primary teeth shifted proximally, regardless of the extent of modification of the finger, in turn weakening the hypothesis that the fondal notch denticles are reduced primary teeth. This is further supported by the coincidence of vestigial primary teeth and fondal notch denticles (e.g., pls. 76C, 77D). The teeth/denticles in the fondal notch clearly do not include the primary teeth of the median series on the fixed finger but it remains unclear as to whether they are homologous to the retrofondal apical (RFA) teeth in females or independently derived serially homologous apical teeth. Although usually exceeding the maximum number of three RFA teeth recorded in females, the fondal notch teeth/denticles of eremobatid males are positionally similar and therefore considered RFA teeth, pending evidence to the contrary. Consequently, it may also be concluded that the fondal notch of eremobatids (fig. 7A, B) is not homologous with the medial notch of other taxa, e.g., Ammotrechidae and Solpugidae (fig. 7C, D).

GALEODIDAE: The teeth on the fixed (dorsal) finger of male Galeodidae usually appear worn, often merging into a low, crenulate margin or "lobulate crest" (pls. 62B, 63A; Pocock, 1900b; Kraepelin, 1908a). Individual teeth may be identified in most species, even if "weak or almost obsolete" (Pocock, 1900b: 136), especially by application of the criteria in table 7.

The typical galeodid dentition (pls. 23M, N, 24C, 25D, 59–63, 64K, L) comprises all primary teeth, one or two submedial (FSM) teeth, and a single subdistal (FSD) tooth on the fixed finger (table 10). In males, the FSD tooth may be difficult to distinguish from the FD and FM teeth when all three are reduced to a crenulate margin. One to four submedial (MSM) teeth occur on the movable finger (e.g., Roewer, 1934: 511, 521; Birula, 1938: 116, fig. 75), a large number for a taxon that does not display any multidentate characters. Both the FSM and MSM teeth increase in size proximally (table 8). Panouse (1964) observed that the number of fondal teeth in both sexes of *Othoes* is stable interspecifically, with two teeth in the profondal (PF) series and four in the retrofondal (RF) series, the latter including a small proximal tooth on the basifondal margin. The same pattern was observed in *Galeodes* and *Paragaleodes* Kraepelin, 1899 specimens examined in the present study. The basifondal (BF) teeth of galeodids are relatively well developed (pl. 64K, L; Panouse, 1964: 51, fig. 1). Unlike male dentition, the female dentition of galeodids remains distinctly differentiated, but wear may be pronounced in older specimens (pl. 60E).

Galeodid dentition patterns were incorporated in species diagnoses by various authors (e.g., Caporiacco, 1944) and rigidly applied by Roewer (1934: 509), who regarded the number of secondary teeth as a criterion for separating species, a view largely abandoned by later authors (e.g., Turk, 1960), as here. The general uniformity in galeodid chelicerae (Panouse, 1964) has resulted in a limited number of illustrations and often very broad descriptions. Consequently, the literature was of limited utility for evaluating dentition patterns or comparison with material examined in the present study.

GYLIPPINAE: A distinct dentition pattern is evident in Gylippinae (pls. 23G, H, 24E, 25F, 85A–F, 86, 90A, B). The male chelicerae of *Gylippus* and *Acanthogylippus* superficially resemble those of typical Eremobatidae in the shape of the manus and fixed (dorsal) finger, the vertical position of the fondal teeth, and the reduced dentition on the fixed finger. A fixed finger proximal (FP) tooth is evident in *Gylippus* (*P.*) *monoceros* Werner, 1905, with a distinct, but smaller tooth situated distal directly adjacent to the FP tooth at its base. Two vestigial teeth, barely visible in *G.* (*P.*) *monoceros*, are situated distal to these teeth. Patterns of dental overlap suggest that these reduced teeth are the fixed finger medial (FM) and distal (FD) teeth (pl. 86C, D). This is supported by immature and female dentition patterns (e.g., pl. 85C–F), in which regular FP and FM teeth are present on the fixed finger, separated by a small submedial (FSM) tooth, situated close to the FP tooth and resembling the tooth at the base of the FP tooth in males. The latter, referred to as the fixed finger submedial (FSM) tooth, appears to be positionally homologous with the FSM tooth of many male Solpugidae (e.g., pl. 109). This fixed finger dentition pattern, comprising a distinct FP tooth with a distinct FSM tooth at its base, and with vestigial FM and FD teeth situated distal to the FSM tooth, is typical of Gylippinae (e.g., Roewer, 1934: 311–318; Birula, 1938; Gromov, 1998).

HEXISOPODIDAE: No attempt has previously been made to identify or homologize the dentition of Hexisopodidae (pls. 24B, 25C, 128–131). Male dentition is highly modified and reduced in this family. Whereas the median series of the fixed finger is situated on a distinct, narrow gnathal edge in all female and all non-hexisopodid male solifuges, the gnathal "edge" of the fixed finger is a broad, blunt surface in male Hexisopodidae (pl. 126C, 128B). In some males, two parallel toothlike rows are present, one at the base of the flagellum and another on the retrolateral surface. In addition to considerable intrinsic variation in the number of smaller teeth or denticles on both fingers, wear induced by burrowing may further contribute to intraspecific variation in hexisopodid dentition (e.g., Wharton, 1981).

Female dentition is more conserved than that of males, and may assist in understanding the dentition of male hexisopodids. Applying the first three criteria of primary homology outlined in the present contribution (table 7), female and juvenile hexisopodids bear a large medial tooth on both the fixed (FM) and movable (MM) fingers, which is at least twice the size of the other primary teeth on each finger, and secondary teeth are absent on the fixed finger and, if present, vestigial on the movable finger (pls. 126F–H, 128D–F). The distinctly larger medial teeth on both the fixed and movable fingers are unique within the order.

As a consequence of what appears to be a proximal shift, the median series teeth of male hexisopodids are situated toward the fondal area. In the male *Chelypus hirsti*, three distinct primary teeth are situated close together near the base of the flagellum, toward the retrolateral side of the gnathal edge (pls. 129C–F, 130A–C). The fixed finger medial (FM) tooth is the largest, in accordance with the patterns of females and juveniles. A smaller but distinct fixed finger distal (FD) tooth is situated distal to the FM tooth, with three equally spaced subterminal (FST) denticles situated distal to that (not indicated in pl. 130A–C). Parallel to the "regular" teeth, which are situated on the retrolateral side of the gnathal edge, a prolateral toothlike ridge, referred to here as the **prolateral dental process (PLDP)**, is situated near the base of the flagellum (pl. 130A). This prominent process, recognized by Hewitt (1931) as the functional row of teeth, restricts movement of the flagellum past a certain point of rotation. The positions of the primary teeth (on the retrolateral side of the gnathal edge) and the presence of a dental process near the base of the flagellum (on the prolateral side of the gnathal edge) were similar in other *Chelypus* species examined: *C. lennoxae*, *C. shortridgei* Hewitt, 1931, and two unidentified species. The dentition was generally less developed in *C. shortridgei* (pl. 129G, H), which differed further in the shape of the prolateral dental process. Manual rotation of the flagellum revealed that the process prevents rotation past a certain point, suggesting that it may function to prevent damage to the flagellum during burrowing.

The fixed finger dentition of male *Hexisopus* species examined in the present study (pls. 127A, B, D, 128B, C), i.e., *H. aureopilosus* Lawrence, 1968, *H. lanatus* (C.L. Koch, 1842), *H. moiseli* Lamoral, 1972, and *H. pusillus*, was more reduced than that observed in species of *Chelypus* (pl. 130). This may not be true for all *Hexisopus* species, however, e.g., Wharton (1981: 48) described the dentition of the fixed (dorsal) finger of *H. fumosus* Lawrence, 1967, as "relatively well developed." Fixed finger primary teeth may be identified in *Hexisopus* by comparison with the positions of the primary teeth, and the relative size of the FM tooth in *Chelypus*. A ridgelike process at the base of the flagellum, similar to the prolateral dental process (PLDP) of *Chelypus*, observed in all *Hexisopus* specimens examined, was variously referred to as a protuberance bearing teeth (e.g., Lamoral, 1972; Wharton, 1981) or as a single tooth (e.g., Wharton, 1981), and is interpreted here as homologous to the prolateral dental process (PLDP) of *Chelypus*. This dental process differs from the PLDP of *Chelypus* because it appears to be more distinctly composed of individual teeth (fig. 2A, pls. 2A, 127D) and does not appear to restrict movement of the flagellum. Also unlike *Chelypus*, no teeth are present on the retrolateral side of the broad gnathal edge. It is hypothesized that the primary teeth of *Hexisopus* are situated on the prolateral side of the gnathal edge, rather than on the retrolateral side as in *Chelypus*, and are fused to the positionally homologous dental process (PLDP). This hypothesis is supported by the observation that one tooth on the dental process of *Hexisopus* is more prominent, and situated in a similar position to the FM tooth of *Chelypus*, with which it is probably homologous. The prolateral dental process (PLDP) appears to comprise many teeth, e.g., "series of 3–6 small teeth on low ridge adjacent base of flagellum, number and size of teeth variable" (Wharton, 1981: 51), two of which are interpreted here as the FM and FP teeth.

One to three clearly identifiable teeth are present on the movable (ventral) finger of hexisopodids (pls. 126D, E, 127E, 128A, 129, 130F, G; Wharton, 1981). *Hexisopus* males appear to possess fewer teeth, "at most two" compared to *Chelypus* males with "at least three," according to Wharton (1981: 45, 48), but these may be very reduced and the patterns and numbers of teeth are not always clear. A **prodorsal serrate carina** or **prodorsal granular tooth**, in *Chelypus* and *Hexisopus*, respectively, is slightly offset prolaterally from the gnathal edge of the movable finger, and may prove to be synapomorphic for the respective genera, or at least for species groups within them. The serrate carina of *Chelypus* is situated slightly more distal with respect to the teeth on the gnathal edge, and often parallel to a serrated distal gnathal edge. The prodorsal serrate carina bears denticulate projections with various degrees of differentiation (pl. 130F, G), which have been referred to as a "row of minute inner teeth" (Purcell, 1902: 225), "row of minute teeth forming serrate ridge," or "inner side of lower jaw near fang tip with a row of 4 small teeth" (Lawrence, 1955: 173), "keel bearing four to six very small teeth" (Lamoral, 1973: 96), and "distally placed mesal row of denticles" (Wharton, 1981: 45). The status of this structure as a generic-level diagnostic character (Wharton, 1981), and its homology among different species should be further examined. An additional granular tooth situated prodorsally, opposite the medial (MM) tooth in some species of *Hexisopus* (pls. 126D, E, 127E, 128A; Wharton, 1981), referred to as the prodorsal granular tooth, was observed in all *Hexisopus* examined in the present study. Although usually referred to as a tooth, this structure is not homologous with the median series of the movable finger. Its position and granular character suggest that it is not homologous with the prodorsal serrate carina of *Chelypus* either.

The hexisopodid genera, *Chelypus* and *Hexisopus*, can be separated by two distinct characters of cheliceral dentition. In *Chelypus*, the median series on the fixed finger is situated on the retrolateral side of the gnathal edge, parallel to a prolateral dental process (PLDP) at the base of the flagellum whereas, in *Hexisopus*, the median series teeth are hypothesized to be fused with the PLDP (pl. 131). In addition to the median series teeth, either a prodorsal serrate carina or a prodorsal granular tooth is present on the movable finger in *Chelypus* and *Hexisopus*, respectively.

A characteristic row of small, regularly spaced, beadlike denticles lining most of the ventral edge of the basal fondal margin (pl. 131) may be a unique synapomorphy for Hexisopodidae. These denticles bear some resemblance to the serrations (crenulations) often present at the base of the fondal series of other taxa, especially eremobatids. Until evidence is presented to the contrary, the beadlike denticles are interpreted here as reduced retrofondal teeth (see section on Dentition Terminology).

Karschiidae: Karschiidae (pls. 23A–D, 24P, 25R, S, 50–55, 64A–H) contains species with truly multidentate chelicerae (pl. 53), typified by male *Eusimonia*, and many species of *Karschia* with a tendency toward a multidentate condition. Fixed and movable finger subterminal (FST and MST) denticlelike teeth and movable finger subproximal (MSP) denticlelike teeth are common among karschiids, especially females (pls. 50G, H, 51D, 52C, D). According to Gromov (2002: 82, 2003a: 84), the teeth of Karschiidae are of limited taxonomic value due to variation in number, size, and shape within series. Gromov (2002, 2003a) therefore described the dental patterns of karschiids broadly, in terms of the range in number of teeth. Irrespective of whether Gromov's (2002, 2003a) assertion proves valid, it can be evaluated only once primary and secondary teeth are identified, a task more achievable for multidentate taxa than previously recognized.

Roewer (1934: 296, fig. 223, reproduced in pl. 28) apparently identified the primary teeth of female Karschiidae on the basis of size, and numbered them I–V. Based on relative size and sclerotization, and supported by reciprocal illumination of criteria 1–4 (table 7), a different interpretation is proposed here for many of the species illustrated by Roewer (1934), e.g., *Karschia* (*K.*) *mastigofera* Birula, 1890 (pls. 28J, 51E).

The typical pattern in Karschiidae includes one or two subdistal (FSD) teeth and one or two submedial (FSM) teeth on the fixed finger. Additional labile, seemingly "randomly" situated denticles may be present in *Eusimonia* (figs. 19, 20). Up to three FSM teeth may be present in *Karschia* (Birula, 1938: 57, 66, figs. 32, 42, 48). The most common pattern, however, is a single FSD tooth and two FSM teeth. Up to three movable finger submedial (MSM) teeth are present, although the MSM teeth of males are often reduced or indistinct (table 10; Birula, 1938). Size gradations are evident in the secondary teeth of the fixed finger, which increase in size proximally, and the movable finger, which increase in size distally (table 8). Unlike the pronounced profondal (PFM and PFP) teeth in multidentate Melanoblossiinae (pl. 159), the profondal (PF) teeth tend to be reduced in multidentate Karschiidae (pl. 64A–H). For example, examination of both chelicerae in three male specimens of *Eusimonia divina* revealed that the profondal teeth are absent in two, and represented by a single denticle in the third. The number of retrofondal (RF) teeth, including retrofondal apical (RFA) teeth, is generally at the upper end of the range for the order (pls. 23A–D, 64A–H), but varies among species.

Female dentition is relatively similar among karschiid genera, but male dentition differs between *Karschia* and the other genera, *Barrus*, *Barrussus*, and *Eusimonia* (pls. 50–55). The primary, secondary, and fondal teeth are more differentiated and the spacing among the teeth more irregular on the fixed finger of male *Karschia* (pl. 50B, F), unlike the other genera, which exhibit a typical multidentate fixed finger.

Lipophaginae: The dentition of Lipophaginae (pls. 23I–L, 24F, 25G, 87–89, 90C–F) is complex and challenging to interpret, for several reasons. An unusually large retrofondal proximal (RFP) tooth, often similar to or larger than the primary teeth (e.g., Wharton, 1981) may be synapomorphic for lipophagines. In addition, the similar size of the fixed finger proximal (FP) tooth and the apical tooth in the retrofondal (RF) row, as well as the closure of both teeth distal to the movable finger proximal (MP) tooth, obscure the boundary between the median and fondal series, as observed by Wharton (1981: 39), who stated "apical teeth in outer cheek series not readily distinguishable from main series in some species." Another peculiarity is the large structure situated distally on the gnathal edge of the fixed finger of *Trichotoma michaelseni*, which may be interpreted in different ways (cf. pl. 88B and 88C). The structure was traditionally interpreted as a large, distally directed FD tooth (e.g., Roewer, 1941; Wharton, 1981; pl. 88B, indicated with an "X"). In the present study, this structure was reinterpreted as the FT tooth at the tip of the fixed finger, with a dorsal hornlike process fused to the dorsal surface of the fixed finger (pl. 88C, indicated with a check mark). This interpretation is briefly discussed, with the teeth and toothlike structures labeled 1–6 from distal to proximal on an illustration of the chelicera of the male *T. michaelseni* (pl. 88B). Teeth 3, 5, and 6 are similar in size, with 3 and 5 separated by a small tooth (4). Patterns of overlap with teeth of the movable finger (criterion 3, table 7) suggest that tooth 6 is the FP tooth. This interpretation does not accord, however, with the conserved pattern of the relative size and number of teeth observed in both the median and fondal series of the female. A more parsimonious interpretation is therefore that tooth 5, rather than 6, is the FP tooth. This differs from previous interpretations (e.g., Wharton, 1981), which identified tooth 6 as part of the median series.

Once the FP tooth has been identified, the remaining teeth of the median series are readily identified in most species except *T. michaelseni*, for which two alternative hypotheses may be considered: (1) tooth 2 is a subdistal secondary (FSD) tooth and structure 1 is a large, distally directed distal (FD) tooth (pl. 88B), or (2) tooth 2 is an FD tooth and structure 1 a large, distally projecting process in addition to the regular teeth of the median series (pl. 88C). Neither hypothesis is supported by the pattern of dental overlap (criterion 3), but the second hypothesis is consistent with the female dentition of *T. brunnea* and *T. michaelseni* (pl. 88F, G) and therefore adopted in the present study. This hypothesis is further supported by an observation by Wharton (1981: 43) that the "fourth tooth" (FSM tooth in pl. 88C) was absent in one of the four males examined. Interpreting tooth 2 as a subdistal tooth according to the first hypothesis implies that a subdistal tooth is present in the absence of a submedial tooth, a pattern not observed in the present study (see fig. 17C). Consequently, by adopting this second hypothesis, the structure previously identified as a large, distally directed distal tooth in *T. michaelseni* (Kraepelin 1914: 132; Hewitt, 1919b: 65; Roewer, 1941: 115) and *T. fusca* Roewer, 1941 (Wharton, 1981: 43), is actually the fixed finger terminal (FT) tooth, i.e., the apex of the fixed finger, the tooth traditionally identified as a secondary (FSD) tooth is the distal (FD) tooth (pl. 88C), and what appears to be the apex of the fixed finger is a cuticular outgrowth of the dorsal surface of the chelicera, similar to the dorsal hornlike processes on the fixed fingers of male Karschiidae. The conclusion that the apparent "apex" of the fixed finger is a separate structure, fused to the dorsal surface of the finger is consistent with the presence of a longitudinal groove (sulcus) separating it from the FT tooth on the pro- and retrolateral surfaces (pl. 88C). Further support for this interpretation is provided by the ventral surface of the terminal tooth (FT), which possesses the typical gnathal edge carina flanked by the pro- and retrolateral carinae characteristic of the mucra of the fingers, whereas the fused hornlike process is smooth all around (fig. 6C). According to this interpretation, the diagnostic character separating *Lipophaga* and *Trichotoma* is therefore not a smaller distal (FD) tooth (Wharton, 1981), but rather the absence of a hornlike process fused to the dorsal surface of the fixed finger.

It may therefore be concluded that the typical pattern of dentition in Lipophaginae includes a single FSM tooth and one (*Bdellophaga* and *Lipophaga*) or no (*Trichotoma*) FSD teeth on the fixed finger, and a single medial (MSM) tooth on the movable finger (pls. 24F, 25G; table 10).

Melanoblossiinae: The dentition of Melanoblossiinae (pls. 23b, c, 24Q, R, 25T, U, 154–159) includes the best examples of multidentate dentition, e.g., the fixed finger of female *Lawrencega minuta* (pls. 154L, 158F), and a tendency toward multidentate dentition, e.g., the subterminal (MST) denticles of female *Melanoblossia braunsi* (pl. 155F). The profondal (PF) teeth are more pronounced than the retrofondal (RF) teeth in melanoblossiines (pl. 159), unlike karschiids, which are also multidentate or exhibit a tendency toward the multidentate condition, in which the retrofondal teeth (RF) are more pronounced. Although it may be difficult to distinguish between primary and secondary teeth in multidentate taxa, especially species in which teeth are absent on one of the fingers, structural and positional criteria (table 7) may be applied to formulate hypotheses concerning the identity of the primary teeth as described above for Karschiidae. Criterion 1 (relative size and sclerotization) is the most useful for species in which teeth are absent on one of the fingers, e.g., the female of *L. minuta* (pls. 154L, 158F).

Not all melanoblossiines are multidentate or display a tendency toward the multidentate condition, but male dentition remains challenging to understand, even in these taxa, as it is usually greatly reduced. The approach followed for identifying homologous teeth in melanoblossiine males is illustrated here in two species, i.e., *Melanoblossia braunsi* (pl. 155, with teeth labelled 1–7) and an undescribed species of *Melanoblossia* (pl. 156). The fixed finger dentition is much reduced in both species, and the movable finger dentition relatively distinct with a proximal (MP) tooth and a medial (MM) tooth separated by a smaller submedial (MSM) tooth. Homologous teeth on the fixed fingers of *M. braunsi* and the undescribed *Melanoblossia* sp. may be identified by their unique morphology, cf. teeth 2, 3, and 4, all of which resemble a fold in the surface of the laterally compressed finger, and tooth 6, which is distinctly pointed (fig. 21A). Tooth 6 of *M. braunsi* is hypothesized to be the FP tooth, based on the pattern of overlap of the teeth on the fixed and movable fingers (pl. 155D), and corroborated by the female dentition (pl. 155F, G). In the undescribed *Melanoblossia* sp., however, the movable finger teeth are concentrated proximally on the finger, and the pattern of overlap suggests that 6 and 7 might be the FM and FP teeth, respectively (pl. 156A, C). The dentition of *M. braunsi* is more conserved hence tooth 6 in the undescribed species is more likely to be the FP tooth, despite being situated far distal to the MP tooth when the fingers are closed. If the latter species were examined without comparison to *M. braunsi*, however, tooth 7, rather than tooth 6, would probably be interpreted as an FP tooth, emphasizing the value of taxonomic comparisons (criterion 4, table 7). A second undescribed *Melanoblossia* sp. possesses a prominent structure distally on the fixed finger (fig. 26, pls. 154G, H, 157), which appears to be a subterminal flange (STF) situated distal to a vestigial fixed finger distal (FD) tooth, expressed as a slight, darkened, elevation.

Although the identification of primary teeth is difficult in melanoblossiines, it is possible to formulate hypotheses of dental homology, even in species with complex dentition, by reciprocal illumination of criteria outlined in the present study. The hypotheses presented here merit further investigation, however, based on examination of more species, and larger series.

Mummuciidae: The dentition of Mummuciidae (pls. 23Y–a, 24N, 25N, O, 26, 149E–H, 151, 152, 153I, J) comprises the usual compliment of primary teeth, although either the distal tooth on the fixed finger (FD), e.g., in *Mummucina colinalis* Kraus, 1966, or the medial tooth on the movable finger (MM), e.g., in *Mummucia mauryi* Rocha, 2001, may be reduced (pl. 149F; Kraus, 1966: 183, figs. 2, 3; Xavier and Rocha, 2001: 130, fig. 3). One or two submedial (FSM and MSM) teeth are present on the fixed and movable fingers. A subdistal tooth (FSD) may be present or absent (pls. 26, 151–153). In a series of *Uspallata* cf. *pulchra* males examined during the present study (pls. 26, 152), the primary teeth were stable in position, size, and shape (e.g., consistent proximal curvature of the apices of individual teeth), with variation limited to the secondary and fondal teeth (see section on Taxonomic Significance and Intraspecific Variation in Dentition). Unlike Ammotrechidae, a movable finger prolateral (MPL) tooth is absent in Mummuciidae (Maury, 1984).

Mummuciidae includes species that share a tendency toward the multidentate condition, including *Mummucia coaraciandu*, *M. mendoza* Roewer, 1934, *M. taiete* Rocha and Carvalho, 2006, *Mummucina masculina* Lawrence, 1954, and *Uspallata* cf. *pulchra*, characterized by relative homogeneity in size of the primary and secondary teeth, and regular spacing between the teeth. Besides presenting characters similar to multidentate taxa, these species share similarities in the shape of the dentition, especially concerning the proximal curvature of the apices of individual teeth. Such similarities, evident in, e.g., *Uspallata* cf. *pulchra* (pls. 26, 152) from Chile and *M. coaraciandu* from Brazil (Martins et al., 2004: 2365, fig. 3A), might be due to convergent evolution, perhaps related to microphagy, or to phylogenetic relationship, but this cannot be evaluated because mummuciid taxonomy is in disarray (Maury, 1998; Xavier and Rocha, 2001; Martins et al., 2004; Rocha and Carvalho, 2006; Botero-Trujillo, 2014).

Rhagodidae: The typical rhagodid dentition (pls. 23E, F, 24A, 25B, 56C–H, 57C, D, 58, 64I, J) comprises all primary teeth, i.e., three teeth (FP, FM, and FD) on the fixed finger and two teeth (MP and MM) on the movable finger. Whereas the proximal (FP and MP) teeth are well developed on both fingers, the distal tooth on the fixed finger (FD) and the medial tooth on the movable finger (MM) are greatly reduced (pl. 57C, D) or absent (e.g., Turk, 1960: 121, fig. 9). Due to its small size, the MM tooth superficially resembles a secondary tooth, but positional criteria, specifically the pattern of dental overlap (pl. 58D) and corollaries of criterion 1 (secondary teeth are more likely to be absent than primary teeth), suggest that it is a primary tooth. The interpretation of a large MP tooth and a very small MM tooth as the only teeth on the movable finger is followed by most workers (e.g., Birula, 1905; Roewer, 1934: 264) but not all, e.g., Kraepelin (1901: 30). Secondary teeth are absent in rhagodids. Rhagodids possess five to seven retrofondal (RF) teeth (pls. 23E, F, 64I, J). Individual RF teeth are readily homologized across the family. A few small, distinct basifondal (BF) teeth are usually present (pl. 64I, J; Pocock, 1889). A distinct movable finger prolateral (MPL) tooth (Roewer, 1934: 264) and prolateral carina (MPLC) occur on the movable finger in both sexes (pl. 58B). As with Galeodidae, but to an even greater extent, the uniformity in rhagodid chelicerae has resulted in very few published illustrations, greatly limiting a literature survey of the dentition patterns in this family.

Solpugidae: Dentition in Solpugidae is relatively conserved compared to other Solifugae families (pls. 23Q, R, 24G, H, 25H, I, 90G–L, 97–125). Sexual dimorphism varies from minor with dentition reduced in both sexes, e.g., *Solpugiba lineata* (pl. 110A–D), through minor with dentition barely reduced in males, e.g., *Zeria sericea* (Pocock, 1897) (pl. 116E–H), to major with dentition modified and greatly reduced in males, e.g., *Solpugista bicolor* (pl. 110E–H). Modifications in male dentition concern the size, shape, and relative positions of teeth. Regardless of the extent of modification, however, five primary teeth are always present and easily identified, usually with some agreement in the number and relative sizes of teeth between sexes in many taxa, although there are exceptions.

The dentition on the movable (ventral) finger of Solpugidae comprises proximal (MP) and medial (MM) teeth. The MM tooth is usually only slightly smaller than the MP tooth. One to three submedial (MSM) teeth separate the MP and MM teeth. The most common pattern on the movable finger is a single submedial (MSM) tooth (table 10), situated closer and usually directly adjacent to the MP tooth. Two or three MSM teeth are present in a few species, e.g., *Solpuga bovicornis* Lawrence, 1929, *Zeria fusca* (C.L. Koch, 1842), and *Zeria zebrina* (Pocock, 1898) (pl. 116D; Roewer 1934: 445, fig. 293a; 448, fig. 295b; 496, fig. 310d). In specimens with three MSM teeth, these secondary teeth are situated in a row along the distal margin of the MP tooth (pls. 116D, 117C).

The typical dentition on the fixed finger of Solpugidae usually comprises one or sometimes two submedial (FSM) teeth and no (rarely one) subdistal (FSD) teeth (table 10). For example, within a population of *Metasolpuga picta* (Kraepelin, 1899), Wharton (1981: 67) reported "at least one" small FSD tooth in 50% of females (*N* = 18). Wharton (1981) recorded variation in the fixed finger dentition of *Solpugista bicolor* (*N* = 12 females; *N* = 21 males) as follows: one FSD tooth and two FSM teeth in all females and seven males, but with the second FSM tooth in males often restricted to one chelicera; one FSD tooth and one FSM tooth in three males; and no FSD teeth and one FSM tooth in 11 males. The male depicted in plate 110F bears no FSD teeth and one FSM tooth, whereas the female depicted in plate 110H displays the same pattern as the females reported by Wharton (1981). Sexual dimorphism in the "typical" dentition pattern therefore appears to be present in *S. bicolor*. The termitophagous *Solpugiba* Roewer, 1934 is unique among Solpugidae due to its large number of fixed finger secondary teeth. Both sexes of *Solpugiba lineata* depicted in the present study (pls. 110A–D, 111) bear two FSD teeth and five FSM teeth, two of which are denticles. The counts for this species fall within the intrapopulation ranges of one to three FSD teeth, and two to four FSM teeth, reported by Wharton (1981). The additional denticles were found to be less common in seven juvenile *S. lineata*, five in the three-malleoli stage, for which the most common pattern in the median series of the fixed finger was FD-(1)-FM-(2)-FP. Exceptions were present in two specimens: the second FSM tooth was absent from both chelicerae of one specimen and a denticle situated proximal to a larger FSD tooth was present on both chelicerae of a second specimen.

FSD teeth are rare in Solpugidae and usually comprise small, variable teeth or denticles. FSM and MSM teeth increase in size proximally in the species with more than one FSM tooth, and in the few species with more than one MSM tooth (table 8). In *S. lineata,* FSM teeth increase in size proximally when labile teeth, usually denticles, are ignored. Such denticles were found to be more common in adults than immatures.

Whereas the fixed finger proximal (FP) tooth is usually the largest primary tooth on the fixed finger in Solifugae (but see Ceromidae and Hexisopodidae above), the fixed finger medial (FM) tooth is often distinctly larger than the other primary teeth in the solpugid genus *Zeriassa*. The FM tooth can be especially pronounced in females and juveniles (pl. 124E, F). Simonetta and Delle Cave (1968: 171, fig. 6) also mentioned a large FM tooth in various species of *Zeriassa*. A similarly large FM tooth occurs in *Solpugisticella* (pl. 124G, H), which appears to be closely related to *Zeriassa* (Turk, 1960).

A prolateral (MPL) tooth on the movable finger has been recorded in only a few solpugid species, i.e., the females of *Ferrandia robusta*, *Zeriassa furcicornis* Lawrence, 1929, and several species of *Solpugassa* Roewer, 1933, including *S. furcifera* (Kraepelin, 1899) and *S. rudebecki* Lawrence, 1961 (pls. 104A, C, E, 105A, C, 124C, 125C; Roewer, 134: 429; Lawrence, 1954: 117, fig. 4C; Lawrence, 1961). An MPL tooth is absent in the male of *Z. furcicornis*. Wharton (1981) recorded an MPL tooth in a male *Solpugassa furcifera*, and a distinct MPL tooth was observed in females of this species in the present study (pl. 104C).

Solpugema (e.g., pl. 109) is characterized partly by the large toothless medial notch on the fixed finger (Roewer 1934: 420), between the proximal (FP) and submedial (FSM) teeth (fig. 7C). A typical dentition pattern associated with the medial notch is a large proximal (FP) tooth, situated directly proximal to a much smaller submedial (FSM) tooth, which is sometimes situated on the base of the FP tooth, e.g., in *S. derbiana* Pocock, 1895 (pl. 108F). The FP tooth and its associated FSM tooth are situated proximal on the finger, whereas the two distal primary (FM and FD) teeth are situated relatively close to one another, more distally toward the apex of the finger.

A small to significant subterminal flange (STF) is situated on the gnathal edge of the fixed finger, toward the distal end of the mucron, in many *Solpugema* (pls. 107A, 109B, D, E, arrows). This flange may resemble a tooth and was often interpreted as such (e.g., Kraepelin, 1900; Lawrence, 1931: 133). Application of the criteria in table 7 suggests that this flange does not belong to the median series teeth, however. Kraepelin (1901: 61) also excluded it from the regular set of teeth, referring to it as an additional *Höckerzahn* ["tooth cusp"] in *Solpugema lateralis* (C.L. Koch, 1842).

Summary of Dentition

Classifying teeth as primary, secondary, and fondal, and evaluating each type independently for intrinsic (inherent) variation reveals more stable patterns than previously suggested in the literature, with implications for taxon diagnosis, description, and phylogenetic analysis. The appearance of variation caused by wear, abnormalities, or misidentifications, should not be misconstrued as intrinsic variation, however. Although relatively common in Solifugae, intrinsic variation in dentition, including bilateral asymmetry in a single individual, is largely predictable whereas wear or deformity is usually random.

Several authors previously suggested that the secondary and fondal teeth are more likely to vary than the primary teeth, but the present contribution is the first to formally survey variation in dentition and analyze where it can be expected. Variation was found to be more common among secondary teeth and fondal teeth than among primary teeth, among small rather than large teeth and, within the median series, among distal rather than proximal teeth. Some species appear to have a greater propensity for variation than others. However, within the sexes of any particular taxon, primary teeth appear to be largely stable in number, relative size, shape, and, often, position, except when these teeth are mostly vestigial. Although variable in size and number, fondal teeth were more consistent intraspecifically than expected based on the literature, with variation restricted largely to specific teeth, in particular the retrofondal submedial (RFSM), retrofondal subproximal (RFSP), profondal submedial (PFSM), profondal subproximal (PFSP), and some retrofondal apical (RFA) teeth. Within categories of secondary (FSD, FSM, and MSM) teeth, teeth increase in size distally or proximally, creating taxon-specific patterns of size gradation (table 8). Recognizing these patterns within the FSD, FSM, and MSM categories may be of value for evaluating variation among the secondary teeth, and for proposing hypotheses of primary homology within these categories.

Except in rare cases, e.g., *Lawrencega minuta*, the dentition of females is too conserved to provide sufficient characters for species, or even generic diagnosis. Unique patterns in male but also female dentition have been identified in some or all members of certain families (pls. 23, 24; tables 8, 10), however, providing potentially informative higher-level characters, especially in conjunction with characters concerning cheliceral shape and size gradation patterns. Examples are the medial (FM and MM) teeth, which are the most prominent primary teeth in Hexisopodidae (pls. 126–130); a large retrofondal proximal (RFP) tooth, often larger than the primary teeth, in Lipophaginae (pls. 87–89, 90C, D); a tendency toward the multidentate condition, such as a greater number of secondary teeth and the presence of subterminal teeth on the mucra in some Eremobatidae (pl. 70J); and the absence of secondary teeth in the median series combined with a larger number of fondal teeth in Rhagodidae (pls. 56C–H, 58, 64I, J).

Taxon-specific trends, often applicable to both sexes, include the following: the predominantly multidentate condition in Karschiidae and Melanoblossiinae; the interspecifically uniform dentition and absence of secondary teeth in Rhagodidae; the "worn" appearance of the dentition of males in most species of Galeodidae; the tendency toward a multidentate condition, including a relatively large number of secondary teeth, in Eremobatidae; two flangelike carinae with various degrees of modification, situated parallel to each other and distal to the movable finger medial (MM) tooth in male Ceromidae; and the large, well developed fixed finger medial (FM) and movable finger medial (MM) teeth, relative to the other primary teeth, on both fingers, and the prolateral dental process (PLPD) of Hexisopodidae.

Intraspecific variation is largely restricted to the secondary and fondal teeth. Delimiting species based on the secondary or fondal teeth of singletons should therefore be avoided. In the presence of large series, however, dentition patterns, including position and number of secondary teeth, and size gradation of teeth within a category, may provide valuable characters from the species to family levels.

The attempt to identify and define homologous teeth through explicit, objective criteria presented here offers several advantages. It will (1) reduce conflicting and/or subjective coding of morphological characters, resulting in more informative matrices; (2) facilitate more concise, accurate, and comparable descriptions of species and supraspecific taxa; and (3) provide landmarks for other hypotheses based on positional homology concerning, e.g., the male flagellum, or flagellar complex, an important character system in all aspects of solifuge systematics.

MALE FLAGELLUM AND FLAGELLAR COMPLEX

Background

The solifuge flagellum, situated on the fixed (dorsal) finger of the chelicera of the adult male (Kraepelin, 1901), is a highly modified seta (Bernard, 1896; Sørensen, 1914; Hewitt, 1919b; Roewer, 1934: 135; Lamoral, 1974), which may take many forms. A **primary flagellum** and a **secondary flagellum**, defined here as a modified ventral flagellar seta (*vfs*) and a modified dorsal flagellar seta (*dfs*) respectively, may be present. Flagella have taxon-specific shapes, including membranous bowl-, husk-, or vesicle-shaped, modified setiform, semisclerotized filiform or straplike, and chitinous spoon-shaped or whiplike flagella. The flagellum was discussed in various levels of detail by Kraepelin (1908a), Sørensen (1914), Hewitt (1919b), Roewer (1934: 135–155), and Lamoral (1975). Roewer (1934: 135–155) presented the most detailed study of flagellar morphology across all solifuge families, and discussed possible mechanisms of flagellar operation through hemolymph pressure. The precise function of the flagellum remains unverified, however. Despite a brief period of doubt (Pocock, 1895; Bernard, 1896), it has long been known that the flagellum is unique to adult males (e.g., Fabricius, 1781, Savigny, 1809: 178; Pocock, 1897: 264; Kraepelin, 1899; Purcell, 1903a; Sørensen 1914: 161; Lamoral, 1975) and this was confirmed by dissections (Dufour, 1861). Dunlop et al. (2004) mistakenly mentioned that the flagellum occurs in both subadult and adult males. Hewitt (1919b: 10) reported the absence of a flagellum in a subadult male *Blossia* and Lamoral (1975) stated that the flagellum is formed during the final ecdysis before becoming adult. Levy and Shulov (1964: 105) observed that the appearance of a flagellum, and the transformation from a "normal" cheliceral shape to the elongated beaklike fixed finger of adult male *Ceratobiton styloceros* occurred in a single molt from subadult to adult male (pl. 137D).

Historical Reference to the "Flagellum"

The term "flagellum" is consistently used in the literature to refer to the single, distinct structure present in male Ammotrechidae, Ceromidae, Daesiidae, Galeodidae, Gylippinae, Hexisopodidae, Mummuciidae, and Solpugidae (pls. 30A, E, G, 32A–G, 34), but is inconsistently applied when more than one distinctly modified structure is present (pl. 30A–D, F). For example, among Karschiidae, a distinct flagellum is usually recognized in *Karschia* (pl. 30A), and referred to as such (e.g., Sørensen, 1914: 174; Roewer, 1934: 146; Gromov, 1998) whereas, in *Barrussus* and *Eusimonia* (pl. 30D), either the dorsal or the ventral structures on the male fixed finger are referred to as "the flagellum" (table 14). In Rhagodidae (pl. 30F), "the flagellum" describes two separate structures with lamellae that overlap to form a unit (Roewer 1934: 55, fig. 50). In Melanoblossiinae (pl. 36G–I), an entire cluster of modified setae is often collectively referred to as "flagellum" (Lawrence, 1972: 98; Wharton, 1981: 53; Gromov, 2003b: 199) or else "flagellum" refers to one particular seta that is slightly more differentiated within the cluster (Purcell, 1903a: 7, 9, figs. 4B, 6; Lawrence, 1935: 86). Roewer (1941: 125) identified a *Flagellum* within the melanoblossiine *Flagellum-Komplex*. In Lipophaginae (pl. 36A–C), the strongly to weakly (depending on the species) modified group of setae at the apex of the fixed finger is collectively described as "the flagellum" (Roewer, 1934: 309; 1941: 115; Wharton, 1981: 39), or as "flagellum absent" (Kraepelin, 1908b: 281; Birula, 1913: 320) or "flagellum not distinguishable" (Purcell, 1903a: 10) when setae of the flagellar complex are barely modified. The cluster of modified setae observed in male Eremobatidae (pls. 37–39) has been described in numerous ways. "The flagellum" may refer to two setae (Banks, 1903: 78) or to a cluster of setae (e.g., El-Hennawy, 1990: 26). Kraepelin (1908a: 223) was the first to recognize a flagellum proper in some Eremobatidae, but the term "flagellum" has rarely been used to refer to a single, distinct seta since then (e.g., Fichter, 1941). More recent workers referred to the eremobatid flagellum as apical plumose seta, bristle or spine (e.g., Muma, 1951, 1970a; Brookhart and Muma, 1981; Brookhart and Cushing, 2002), adding descriptive terms such as "apical plumose bristle," or "subapical plumose bristle" (table 15; Muma, 1951: 61). Muma (1976: 3) identified specific "flagellar setae…usually 1 or 2" hidden among associated setae.

The inconsistent use of flagellum led Selden and Shear (1996: 596) to describe "the flagellum" as

> a complex of structures.... In some, the dorsal side of the base of the fixed finger bears a curious horn or projections. In others, there is a bunch of large setae, which may be plumose or distally expanded, and such setae may extend onto the movable finger. In many genera there is a single organ (flagellum proper, presumably a highly modified seta) which is commonly associated with groups of modified setae.

The absence of an unambiguous definition for the flagellum confounds the question as to whether it is a single, homologous structure in all solifuges or multiple structures, some with independent origins, and has implications for describing and coding morphological characters for diagnoses, descriptions, and phylogenetic analyses from the species level on up. An unambiguous definition of the flagellum and its component structures, however, requires a framework of testable hypotheses of homology, both among its components and across the order.

Flagellar Anatomy

The only histological study of the flagellum, by Lamoral (1975), was based on four species of Solpugidae. Lamoral's (1975) observations were confirmed by cross sections of representative Ceromidae, Hexisopodidae and Solpugidae conducted in the present study (pl. 41E–N). Two canals, extending along the shaft of the flagellum, were identified. The first, referred to as the **flagellar hemolymph lumen (hl)** (hemolymph canal), is connected basally to the hemolymph, and blind ending apically. A connection between the hemolymph and flagellum, through a longitudinal **atrium** at the base of the Solpugidae flagellum, was described by Sørensen (1914: 168, fig. 11c), and depicted in cross section by Roewer (1934: 154, fig. 156; reproduced here in fig. 22D). The second, referred to as the **alembic lumen (al)**, comprises the **alembic canal** in the flagellar shaft and, at least in Solpugidae, the **alembic pouch**, which is a blind-ending pouch into which the canal terminates basally. The pouch transitions into the canal, resulting in a characteristic flask shape that is visible through the cuticle of the **bulbous base** of the flagellum of Solpugidae (pls. 33K, L, 45A). The alembic lumen is lined by epicuticle and hypothesized to have formed by "longitudinal invagination" (Lamoral, 1975: 139) of the seta. There appears to be no connection between the alembic canal and any part of the hemolymph. Lamoral (1975: 139) hypothesized that the alembic fluid is secreted by modified epidermal cells during ecdysis, and the fluid is trapped in the basal pouch (alembic pouch) by invagination of the flagellar cuticle during final ecdysis.

All flagella comprising a shaft, as defined in the present contribution, contain an alembic lumen and a hemolymph lumen (pl. 41E–N). These are visible through the shaft of the flagella of Ceromidae, Hexisopodidae, Solpugidae, and the daesiids, *Ammotrechelis*, *Namibesia*, and, probably *Syndaesia*: one as a distinct canal, clear, and often appearing to contain specs of dirt suggesting an opening to the exterior, the other opaque, often containing patches of a milky, viscous substance, partly surrounding the clear lumen (e.g., pl. 32). In cross sections of the flagellar shaft of a ceromid, a hexisopodid and three solpugid species (pl. 41E–N), the alembic lumen is clearly visible as a well defined circular, apparently empty canal, whereas the hemolymh lumen contains a yellowish substance, and occupies the space between the alembic canal and the flagellar cuticle.

Roewer (1934: 135–155) reported that the **flagellar tip** is closed. Lamoral (1975) was the first to provide evidence for the presence of an opening to the exterior of the alembic canal at the tip of the flagellum in Solpugidae. Indications of an opening in a ceromid and a hexisopodid were also found in the present study (pl. 41G, M, arrows). Maury (1980a: 64, figs. 3, 4, 11) illustrated two openings in the flagellum, one near the base and one at the apex of the shaft, connected by a tube, in *Amacata penai*, currently in synonymy with *Ammotrechelis goetschi*, and *Syndaesia mastix*. When the flagellum of *A. goetschi* was examined in the present study, the external opening at the apex of the flagellar shaft (pls. 32F, 33H, arrows) and a broad, clear alembic lumen (pl. 32F) were distinctly visible. An opening could not be found at the base of the flagellum (pl. 40G), however, and the shaft appears to connect to a blind-ending pouch. The alembic lumen could be traced through the attachment point of the flagellum (pl. 41I, J) into the chelicera of a hexisopid examined. The function of the alembic fluid is unknown, however.

The flagellum of *Dinorhax* contains a lumen, into which the sulcus, extending longitudinally along the flagellum, appears to protrude (pl. 41A). The homology of the flagellar lumen of *Dinorhax* with the alembic lumen and hemolymph lumen in the shaft of the aforementioned taxa is unclear, but an alembic lumen appears to be absent as no external opening is visible at the apex of the flagellum. A cross section of the *Dinorhax* flagellum indicates grooves in the cuticle lining the lumen, and what appear to be small projections reminiscent of the plumosity covering the exterior surface of the flagellum. Although hemolymph appears to extend into the flagellum of *Karschia*, neither an alembic lumen nor an opening at the apex were observed (pl. 30A). The similar external morphology of the flagella of *Dinorhax* and *Karschia* suggests that the flagellum of the former may also contain hemolymph.

An alembic lumen also appears to be absent in the flagellum of galeodids (pl. 41B–D). The lumen continues to the area where the **peduncle** transitions into the **scapus**, but it is unclear whether it is blind ending or opens to the exterior at the base of the scapus. A lumen is absent, or highly vestigial in the scapus (pl. 41D). According to Lamoral (1975: 139) "[e]xamination of a large selection of representative species from [Ceromidae, Daesiidae, Hexisopodidae, Lipophaginae, Solpugidae, and Melanoblossiinae] revealed that all have an alembic canal connected to a basal pouch, thus strongly suggesting that this cuticular structure prevails in all species." Lamoral (1975) discussed and illustrated longitudinal cross-sections of the flagellum of Solpugidae only, however, and it is unclear how the flagella of Daesiidae (excluding *Ammotrechelis*, *Namibesia*, and *Syndaesia*), Lipophaginae, and Melanoblossiinae would accommodate an alembic canal as defined. Only the whiplike flagella exhibit openings to the exterior (e.g., pl. 41G, M), and no fluid other than the milky hemolymph is visible in, e.g., the narrow lumen of the membranous secondary flagellum of *Eusimonia* (pl. 30D). Roewer (1934: 135–155) illustrated cross sections of most flagellar types (some reproduced in fig. 22), but none of his figures indicate a possible alembic lumen. Only a hemolymph lumen, i.e., no alembic lumen, is therefore assumed to exist in the membranous flagella (Ammotrechidae, Mummuciidae, and Daesiidae other than *Ammotrechelis*, *Namibesia*, and *Syndaesia*), the primary and secondary flagella of Rhagodidae and the karschiids, *Barrus*, *Barrussus*, and *Eusimonia*, and the flagella of Galeodidae, *Dinorhax*, and *Karschia*, but more data are needed to verify this. The hemolymph lumen probably functions to change the shape or direction of the flagellum.

Setal Transformation Hypotheses

The structure of the flagellum allows hypotheses to be postulated concerning the transformation from seta to flagellum. Lamoral's (1975) histological studies indicated that the alembic lumen is lined by epicuticle that would most likely be achieved by longitudinal invagination of the seta, providing a mechanism for the formation of the whiplike flagella of ceromids, hexisopodids, solpugids, and three daesiid genera, *Ammotrechelis* (pl. 32F), *Namibesia* (pl. 32E) and *Syndaesia*.

The flagellum of Gylippinae may have developed from a seta that became broad and flattened. Alternatively, based on similarity to the flagellum of Solpugidae, the basal part of the shaft of which is fused to the fixed (dorsal) finger, the flagellum of Gylippinae is probably a remnant of the whiplike flagellum, formed in a similar manner, but with the base, stalk, and possibly the alembic canal secondarily lost.

There are two plausible pathways by means of which the membranous, usually bowl-, husk-, or vesicle-shaped flagella of ammotrechids, most daesiids, and mummuciids (pls. 34, 35) might be formed. Roewer (1934: 138) suggested the membranous flagella may have formed by simple flattening and broadening of the seta. Alternatively, the membranous flagella might have been secondarily derived from the whiplike flagella, by unfolding of the base, loss of the shaft and, possibly, the alembic canal. This hypothesis is suggested by the flagellum of *Ammotrechelis* (pl. 32F), which is intermediate in form between the whiplike and membranous flagella and may have formed by invagination to create the elongated shaft, and subsequent opening (secondary unfolding) of the base.

The flagella of Karschiidae (pls. 30A, D, 31A, B), Galeodidae (pls. 30G, 31F, 41B–D), Rhagodidae (pls. 30F, 31D), and *Dinorhax* (pls. 30E, 31C, 41A) appear to have altered shape without longitudinal invagination: in Galeodidae, by simple compression of the distal part of a seta (although it is difficult to explain the plumosity restricted to the internal surface of the scapus); in *Barrus*, *Barrussus*, *Eusimonia*, and Rhagodidae, by broadening of the seta, for example; and in *Dinorhax* and *Karschia*, by "infurling" longitudinally, i.e., the seta flattened before rolling onto itself, consistent with the longitudinal sulcus and plumose fringe in the flagella of *Dinorhax* and *Karschia,* respectively. Roewer (1934: 145, fig. 156; reproduced here as fig. 22A) hypothesized that, in *Karschia*, longitudinal infurling resulted in a double-membraned flagellum with hemolymph restricted to the lumen between the membranes. Longitudinal infurling does not imply that hemolymph is restricted to a double outer wall, however. A double wall was not observed in the present study, and hemolymph appeared to be present in the lumen of the flagellum. The double wall may have fused in *Karschia*.

TABLE 14
Alternative interpretations and terminology for flagellar structures of the karschiid solifuge genus *Eusimonia* Kraepelin, 1899
Abbreviations: **1°,** primary; **2°,** secondary.

1° flagellum (ventral)	2° flagellum (dorsal)	Dorsal hornlike process	References
flagellum (F)	*lamelle* (L)	*crochet fixe, profondément bifurqué*	Simon (1879: 128, 153, pl. 3, fig. 21) for *E. furcillata* (Simon, 1872)
lame transparente	*flagellum*	n.a.	Simon (1879: 128, 131, pl. 3, fig. 24) for *E. kabiliana* (Simon, 1879)[a]
Flagellum	*das Plättchen*	*Horn des dorsalen finger*	Kraepelin (1901)
Chitinstab/Horn (*Flagellum*)	*das Plättchen* (*Flagellum*)	*Horn des dorsalen finger*	Kraepelin (1908a)
flagellum	vertical lamella	dorsal horn	Hirst (1908: 247)
flagellum ("*kurz, hornartig*")	*einem durchsichtigen senkrechten Plättchen*		Birula (1913: 321)
un procès conique	*plaque*		Sørensen (1914: 174)
Viertelkreishorn	*Bläschenflagellum*	*Gabelhaken/ Chelicerenfingergabel*	Roewer (1934: 143, 299)
Haken	*flagellum/ flagellumplättchen*	*Horn* (*processus rostralis*)	Birula (1935a)
un	fl	rh	Birula (1938: fig. 47)
	lame		Panouse (1955, 1956, 1957)[b]
Viertelkreishorn	*Bläschen-Flagellum*	*Finger ist gegabelt*	Pieper (1977)

[a] Flagellar arrangement of *E. kabiliana* (Simon, 1879) differs from that of other species of *Eusimonia*. The arched structure situated dorsomedially on the fixed (dorsal) finger was illustrated and termed the flagellum by Simon (1879: pl. 3, figs. 23, 24). This species was not examined in the present study.

[b] Panouse (1955: 346) did not provide a specific term for the primary flagellum, but described it as "*un organe egalement mobile.*" Panouse (1956, 1957) regarded this as the same structure referred to by Roewer (1934: 143, 299) as the *Horn* or *Viertelkreishorn*, terms he considered misleading.

The flagella of Eremobatidae (pls. 38, 39) and Melanoblossiinae (pl. 36G–I) are probably secondarily setiform. This hypothesis is partly supported by the atypical position of the prolateral setae that form the flagellar complexes characteristic of both taxa, and especially the melanoblossiines.

Flagellar Morphology and Terminology

No attempt has been made to unify the terminology for different components of a single flagellum. Homologous components, and associated terminology, are proposed here based on structural and positional similarity between different sections of the flagellum, and comparisons with apparently transitional forms, e.g., the flagellum of *Ammotrechelis goetschi*. Three types of flagella, i.e., setiform, sessile, and composite types (table 16), may be identified based on the extent or manner of modification, whether the flagellum is subdivided into components, and whether it can change direction (i.e., rotate) or shape by, e.g., hemolymph pressure.

Setiform Flagellum: The setiform flagellum is relatively uniform throughout, and retains a markedly setiform character and affinities with plumose setae. It is present in Eremobatidae (pls. 38, 39A–F) and Melanoblossiinae ("a" in pl. 36G, I). The flagellum emerges and projects directly from the chelicera without a distinct **flagellar stalk** and base to change its direction, and is unable to change shape by hemolymph pressure.

TABLE 15

Morphology of the flagellar complex in genera of the solifuge family Eremobatidae Kraepelin, 1901 in which adult males are known

Based on Muma (1951, 1989), Brookhart and Muma (1987), Brookhart and Brookhart (2006), Brookhart and Cushing (2008) and the present study. Abbreviations: ***pvsd*****,** proventral subdistal setae; ***vfs*****,** ventral flagellar seta; **fg,** flagellar groove.

Genus	Dorsal series (*pdd*)	Ventral series (*pvd*)	*vfs*[a]	*pvsd*	Groove structure	Groove position	Groove length
Chanbria Muma, 1951	homogeneous; striate, weakly flattened	homogeneous; plumose; elongated	undifferentiated		absent	n.a.	n.a.
Eremobates Banks, 1900	homogeneous; simple, tubular; sometimes striate	homogeneous; plumose; elongated, covers basal part of fg	plumose; conspicuous, flattened; situated in fg[b]		distinct	promedial to proventral	length of finger
Eremochelis[c] Roewer, 1934	homogeneous; simple, tubular	homogeneous; plumose; elongated, covers basal part of fg	plumose; enlarged, flattened (*branchi* group), not conspicuously enlarged (*bilobatus* and *imperialis* groups)		deep narrow slot, without carinae (*branchi* group); distinct, enlarged basally, with distinct carinae (*bilobatus* group); indistinct series of carinae (*imperialis* group)	promedial to proventral	not reaching base of finger (*branchi* group); length of finger (*bilobatus* and *imperialis* groups)
Eremocosta Roewer, 1934	homogeneous; weakly modified	homogeneous; plumose; weakly modified	undifferentiated		ventrodistal concavity	proventral/ventral/ retroventral	short, not extending to base
Eremorhax Roewer, 1934[b]	homogeneous; simple tubular	homogeneous; plumose; unmodified, or simple tubular	undifferentiated		indistinct hollow or crease	ventral to proventral	not extending to base
Eremothera Muma, 1951	heterogeneous; incl. two flattened	homogeneous; plumose; short	undifferentiated	simple, tubular		promedial	short, weak
Hemerotrecha Banks, 1903	homogeneous/ heterogeneous; may be subspiniform	homogeneous	undifferentiated or differentiated		absent; ventrodistal concavity in some[d]	prodistal	short; restricted to apex of finger

[a] Undifferentiated *vfs* implies absence of a flagellum as defined in present contribution.

[b] Muma (1951: 53, fig. 46); Brookhart and Muma (1981: 291, figs. 2, 3).

[c] As *Therobates* Muma, 1951.

[d] Brookhart and Cushing (2008: 50, fig. 3).

SESSILE FLAGELLUM: The sessile flagellum is clearly modified from its original setal form, but unlike the composite flagellum, its development does not appear to have involved a longitudinal invagination along the seta to form an alembic canal (pls. 30, 31). With the possible exception of the karschiid, *Karschia*, the sessile flagellum also bears no obvious homologs to the parts of the composite flagellum, and an alembic canal appears to be absent, based on the absence of an external opening. Sessile flagella are unable to rotate at the point of attachment, except for the flagella of Galeodidae and the karschiid, *Karschia*. The sessile flagellum includes the spoon-shaped flagellum of Galeodidae and both the primary and secondary flagella of Rhagodidae (together forming a compound structure, referred to as a diploflagellum) and the karschiids, *Barrus*, *Barrussus*, and *Eusimonia*. The filiform flagella of *Dinorhax* (Dinorhaxinae) and *Karschia* are tentatively considered sessile flagella because both appear to have formed by longitudinal infurling, rather than invagination, neither is readily rotatable, and an alembic canal, typical of a composite flagellum with a shaft, is not evident (e.g., see cross section of *Dinorhax* flagellum in pl. 41). The sessile flagellum emerges and projects directly from the chelicera without a stalk, except in *Karschia*. It is able to change direction through rotation around an axis in Galeodidae (Roewer, 1934: 149) but, unlike the composite flagellum that rotates paraxially within its socket, the flagellum of galeodids rotates subdiaxially from a proximally directed position to a prodistally directed position. The flagellum of *Karschia* is able to rotate paraxially within its socket. However, unlike the composite flagellum, which can rotate more than 180°, the flagellum of *Karschia* cannot rotate more than 90°. Based on hemolymph remains visible in the flagellum of some specimens (e.g., pl. 30D, F; Roewer, 1934: 143–144), the flagella of *Eusimonia* and Rhagodidae appear to be able to change shape. The spiral flagellum of *Karschia* and the ventrally directed flagellum of *Dinorhax* are probably also able to straighten with hemolymph pressure based on what appear to be remnants of hemolymph within them (pl. 30A, E).

COMPOSITE FLAGELLUM: A composite flagellum comprises a stalk, base, and shaft (e.g., pl. 33), although some components may be secondarily lost. All composite flagella are probably able to change direction and/or shape, most plausibly through hemolymph pressure (Sørensen, 1914: 167, 169; Roewer, 1934: 135–155; Lamoral, 1975). All three sections (stalk, base, and shaft) occur in the flagella of Ceromidae, some Daesiidae (*Ammotrechelis*, *Namibesia*, *Syndaesia*), Hexisopodidae, and Solpugidae (e.g., pls. 32A–G, 33A–H, K–M; table 16). It is hypothesized that the shaft or homolog thereof is absent in the bowl-, husk-, or vesicle-shaped composite flagella of Ammotrechidae, most Daesiidae (e.g., *Biton*), and Mummuciidae. The flagellum of these taxa therefore comprises a stalk and a base only. The fusion of the flagellum to the dorsal surface of the fixed finger in Gylippinae (pl. 32H, 33I, J) resembles the fusion of the proximal section of the shaft of the flagellum to the fixed finger, between its emergence from the bulbous base until it curves dorsally (e.g., pl. 32G), in Solpugidae. The flagellum of Gylippinae is therefore hypothesized to be a composite flagellum, comprising a modified shaft, with the base and stalk secondarily lost. Alternatively, the absence of a stalk and base may imply that the flagellum of Gylippinae is sessile.

The **flagellar shaft**, when present, is markedly sclerotized, long, and round to laterally compressed and whiplike in composite flagella, with few exceptions. In *Ceromella*, the shaft is broad and semisclerotized to membranous (pl. 33B). A broad, laterally compressed membranous shaft is also present in *Ammotrechelis* (pls. 32F, 33H). The whiplike shape appears to be secondarily modified in a few Solpugidae, taking on clawlike or angular forms (e.g., pl. 49A–C). Except for the reduced shaft of Gylippinae, the shaft of the composite flagella, when present, almost certainly contains hemolymph and alembic canals, the latter opening apically to the exterior (pls. 32, A–G; 41E–N; Lamoral, 1975; Maury, 1980a: 64, fig. 11).

The **flagellar base** is an enlarged section from which the shaft emerges. It is swollen and bulbous in Solpugidae (pls. 32G, 40D), capsular in Ceromidae (pls. 32B, 33B, C), and cuplike in Hexisopodidae (pls. 32C, D, 40F) and two daesiid genera, *Namibesia* (pls. 32E, 40E) and *Syndaesia*. In *Ammotrechelis* (pls. 32F, 33H, 40G), the base is membranous and bowl shaped, resembling the flagellum of ammotrechids (pls. 34E, F, 35F, G) and, to an extent, most other daesiids (pls. 34A–D, 35A–E) and mummuciids (pls. 34G, H, 35H, I). The membranous bowl- or husk-shaped flagella of these taxa are therefore considered homologous with the base of the flagellum of *Ammotrechelis* and taxa with whiplike flagella, a hypothesis first proposed by Hewitt (1919b) and Roewer (1934: 155), who observed similarities between the membranous flagellum of Daesiidae and the whiplike flagellum of Solpugidae.

A short **flagellar stalk** connects the flagellar base to the cheliceral finger (e.g., pl. 40C, F). The stalk varies from relatively distinct, e.g., in Ceromidae, Hexisopodidae, and *Namibesia*, to short and barely identifiable, e.g., in Ammotrechidae, Mummuciidae, and most Daesiidae with membranous flagella. In the daesiid genera, *Ammotrechelis*, *Biton*, and *Gluvia* C.L. Koch, 1842, the membranous stalk attaches to the base in such a manner that a hairpin shape, the "rotatory axis," forming a "triangular" marking according to Lawrence (1928: 267, plate XXIII, fig. 48), is visible through the transparent base (pl. 40G, H, I). The "hairpin" changes direction with the movement of the flagellum because it is located at the transition from the stalk to the base of the flagellum, as evident, e.g., in the orientation of the stalk of a dorsally rotated flagellum (pl. 40H) compared with that of a flagellum in the resting position (pl. 40I). The flagellum of the *crepidulifera* group of *Blossia*, e.g., *B. rosea* (Lawrence, 1935) (pl. 145F), resembles the **peduncle** and **scapus** of the flagellum of Galeodidae (pl. 31E; Lawrence, 1935: 76, fig. 4). The similarity is superficial, however, because both the **flagellar stem**, commonly referred to as the "stalk" (Purcell, 1903a: 5; Wharton, 1981: 28), and the broadened leaflike section of the flagellum of *Blossia*, represent the base of the composite flagellum, whereas the flagellum of Galeodidae, comprising a peduncle and scapus, is sessile. The "stalk" of the flagellum of such species of *Blossia* is not homologous to the stalk of the composite flagellum, hence the term *stem,* or flagellar stem, is preferred in these cases.

An alternative hypothesis proposes that the collar of the flagellum of Galeodidae may be homologous with the base of the composite flagellum, and the peduncle and scapus with the shaft of the composite flagellum (pl. 30G, H). However, unlike the composite flagella, there is no indication of a stalk in the flagellum of Galeodidae, which retains a basic setal morphology, without any indication of longitudinal invagination and without an alembic canal (pl. 41B–D).

Manner of Flagellar Attachment: The point of flagellar attachment to the fixed (dorsal) finger (pl. 40) is distinctly socketlike and paraxially rotatable in Ceromidae, Daesiidae (including *Ammotrechelis*, *Namibesia*, and *Syndaesia*), Hexisopodidae, and *Karschia*; socketlike and subdiaxally rotatable in Galeodidae; and socketlike and nonrotatable in Ammotrechidae, Eremobatidae, Melanoblossiinae, Mummuciidae, and *Dinorhax*. The flagellum is attached to the round or oval, sclerotized inner margin of the socket in Ammotrechidae and Mummuciidae (pl. 40J, K, L). The point of attachment is also socketlike, and the flagellum immovably inserted parallel to the chelicera in Rhagodidae (pl. 40B) and the karschiids, *Barrussus* and *Eusimonia* (pl. 30E). The inner margin of the flagellar socket is often more strongly sclerotized, especially in Ammotrechidae, Ceromidae, Daesiidae, Hexisopodidae, Mummuciidae, and *Karschia*. Unlike in other taxa, the point of flagellar attachment is indistinct in Solpugidae (pl. 40D) and Gylippinae, the flagella of both taxa being immovably fixed to the chelicera.

The stalk of the composite flagellum is usually inserted perpendicular to the chelicera, and connects perpendicular to the flagellar base, enabling the base and stalk to be situated and rotated, if applicable, parallel to the fixed finger on the prolateral or prodorsal surface of the chelicera. Solpugidae, which also possess a composite flagellum, are exceptional: the stalk, which is fused to the chelicera and not clearly visible, appears to be situated in the same axis as the rest of the flagellum, necessitating a deep insertion of the flagellar base into the dorsal surface of the chelicera (pls. 32G, 45). A stalk is absent from the composite flagellum of Gylippinae, which appears to originate from the sclerotized area of the fixed finger (the original point of attachment in the setose area is apparently lost), and remains fused to it for most of its length. A stalk is absent from the setiform flagella of Eremobatidae and Melanoblossiinae and, except for *Karschia*, the sessile flagella of *Barrus*, *Barrussus*, *Dinorhax*, *Eusimonia*, Galeodidae, and Rhagodidae, in which parallel insertion of the flagellum into the fixed (dorsal) finger is accomplished by originating from a slightly elevated area (e.g., in *Dinorhax* and *Eusimonia*) (pl. 30D, E) or from (e.g., in Galeodidae and Rhagodidae) or into (e.g., in Eremobatidae and Melanoblossiinae) a depression, which may take the form of a deep socket, the **alveolus** (e.g., in Galeodidae, *Karschia,* and Rhagodidae) (pl. 30F, H), a groove, the flagellar groove (e.g., in Eremobatidae) (pl. 38), or a shallow depression, the flagellar complex depression (e.g., in Melanoblossiinae) (pl. 36G, I).

Origin of the Flagellum

As originally proposed by Bernard (1896), the flagellum is broadly accepted to be a modified seta (Sørensen, 1914; Hewitt, 1919b; Roewer, 1934: 135; Lamoral, 1974). Its distinct setal character is evident in some taxa but not others, although even in highly modified flagella, like those of Daesiidae, the presumed plesiomorphic plumosity is often retained. Whether there is a single origin for the flagellum, i.e., whether it is homologous across the order, or has multiple origins, remains unknown. Hypotheses concerning flagellar homology are complicated by the great diversity in flagellar structure and position, probably associated with different reproductive pressures (tables 1–4).

Literature: Kraepelin (1908a) and Roewer (1934) each proposed multiple origins of the male flagellum, whereas Hewitt (1919b) proposed a single origin for southern African taxa. Hewitt (1919b) argued that the seta giving rise to the flagellum is homologous across taxa, an idea first put forth by Sørensen (1914), and largely adopted here (pl. 43). Hypotheses of setal modification include thickening of the seta, invagination of the seta, or the fusion of two setae.

Kraepelin (1908a: 220) proposed at least two origins of the flagellum, involving the two basic structures (or setae) that comprise the compound rhagodid flagellum, which was interpreted as the “most primitive,” namely the *Stab* (“rod,” i.e., the dorsal unit of the rhagodid flagellum) and *Schuppe* (“flake,” i.e., the ventral unit) (pl. 42A). Largely based on the shape of these two structures, Kraepelin (1908a) proposed a transformation series for the flagellum of Solifugae (schematic representation provided in pl. 42). According to Kraepelin (1908a), the dorsal unit (*Stab*) is homologous to the rodlike flagellum of Galeodidae (pl. 42B), and the ventral unit (*Schuppe*) to the husklike flagellum of Daesiidae (pl. 42C). According to Kraepelin (1908a), both structures are present in Solpugidae (pl. 42D), but fused into a single structure composed of a bulbous base (*Schuppe*) and a shaft (*Stab*). In *Dinorhax* (pl. 42I) and Hexisopodidae (pl. 42G), the *Schuppe* is reduced, leaving only the filamentous *Stab* to form the flagellum. Kraepelin (1908a) further hypothesized that both *Stab* and *Schuppe* are represented in the flagellar complex of Karschiidae, in *Eusimonia* (pl. 42E) by the upper membranous structure labeled *Plättchen* and the ventral structure (generally referred to as the flagellum), labelled *Chitinstab*, and in *Karschia* (pl. 42F) by the filiform flagellum and the modified setae labeled *Säbelborsten*. However, Kraepelin (1908a) recognized the difficulty of deriving the flagella of Eremobatidae (pl. 42K), Gylippidae, and Melanoblossiinae (pl. 42J) from either the *Stab* or *Schuppe*. The lamelliform flagellum (*Läpp-*

TABLE 16

Types and components of flagella in Solifugae based on hypotheses of homology proposed in present contribution

Abbreviations: **1**°, primary flagellum; **2**°, secondary flagellum.

Taxon	Flagellum	Stalk	Base	Shaft
Ceromidae Roewer, 1933 (*Toreus* Purcell, 1903); Lipophaginae Wharton, 1981	absent	n.a.	n.a.	n.a.
Eremobatidae Kraepelin, 1901 (when present)	setiform	n.a.	n.a.	n.a.
Melanoblossiinae Roewer, 1933	setiform	n.a.	n.a.	n.a.
Dinorhaxinae Roewer, 1933	sessile	n.a.	n.a.	n.a.
Galeodidae Sundevall, 1833	sessile	n.a.	n.a.	n.a.
Karschiidae Kraepelin, 1899 (excluding *Karschia* Walter, 1889) (1° and 2°)	sessile	n.a.	n.a.	n.a.
Rhagodidae Pocock, 1897 (1° and 2°)	sessile	n.a.	n.a.	n.a.
Gylippinae Roewer, 1933	composite	absent	absent	present
Ceromidae (excluding *Toreus*)	composite	present	present	present
Daesiidae Kraepelin, 1899 (*Ammotrechelis* Roewer, 1934; *Namibesia* Lawrence, 1962; *Syndaesia* Maury, 1980)	composite	present	present	present
Hexisopodidae Pocock, 1897	composite	present	present	present
Karschiidae (*Karschia*)[a]	composite	present	present	present
Solpugidae Leach, 1815	composite	present	present	present
Ammotrechidae Roewer, 1934	composite	present	present	absent
Daesiidae (membranous types)	composite	present	present	absent
Mummuciidae Roewer, 1934	composite	present	present	absent

[a] In *Karschia,* structures resembling "stalk," "base" (basal peg), and "shaft" can be identified; their homology with parts of composite flagellum is uncertain.

chen) of *Gylippus* (pl. 42L) is situated toward the apex of the fixed finger, but is connected through a ribbonlike extension to what Kraepelin (1908a) referred to as the "normal attachment point" (*normalen Insertionsstelle* of Kraepelin, 1908a: 222) of the flagellum, suggesting that it may have originated from either of the flagellar components (*Stab* or *Schuppe*). The **setiform flagellar complex principal seta (*sfc principal seta*)**, traditionally interpreted as the flagellum of *Melanoblossia* (a short robust seta within a cluster of modified plumose setae) and Eremobatidae (obscured in a deep longitudinal furrow with differently modified setae on either side), may be derived from either the *Stab* or the *Schuppe*. The flagellum of *Lipophaga* (Lipophaginae) appears to be absent, even when some of the setae are modified. Kraepelin (1908b) concluded, however, that it would be more correct to refer to the reversal of one or both of the original flagellar components to a less modified seta, than to refer to absence of the flagellum in any given taxon. This is also the conclusion of the present study, in which absence is shorthand for absence of a modified seta.

Roewer (1934: 135–155, figs. 126–56) proposed multiple origins of the flagellum, based on an elaborate interpretation of transformations, often within the framework of other morphological characters (e.g., presence or absence of claws on tarsus of leg I, number of leg IV tarsomeres), and within the context of New and Old World taxa. In many parts of the discussion, Roewer (1934) only alluded to similarities between the flagella of different taxa without actually proposing hypotheses of transformation. A summary follows (for illustrations see Roewer, 1934: 136–154, figs. 126–56).

Among New World taxa, the similar positions of setae in the eremobatid flagellar complex suggests a transition from a brush of setae at the base of the fixed finger, to a row of modified dorsal setae, eventually resulting in two enlarged but barely sclerotized, finely fringed setae situated close together and parallel on the fixed finger. One of these setae widens and the margins curl slightly inward to form the flagella of Ammotrechidae and Mummuciidae.

Roewer (1934: 138) proposed various pathways among Old World taxa. The slightly modified setae of Lipophaginae gave rise to the well-defined flagellar complex of Melanoblossiinae. The two flagella of Rhagodidae underwent various transformations. Firstly, the two rhagodid flagella are homologous to the two flagella of *Eusimonia* (Karschiidae). Secondly, based on the interpretation of an apparently bifid flagellum in *Gylippus rickmersi*, currently in synonymy with *Gylippus* (*Anoplogylippus*) *ferganensis* Birula, 1893 (Gylippinae), the two rhagodid flagella gave rise to the two papillae of *G.* (*A.*) *ferganensis*, which eventually fused into the single flagellum of other Gylippinae.

Roewer (1934) pointed out various similarities that might indicate affinities among the flagella of different taxa. For example, the flagellum and associated setae of *Dinorhax* are similar to the flagella of Rhagodidae and additional proventral distal setae. The row of setae covering the base of the flagellum of Ceromidae resembles the flagellar complex of Melanoblossiinae. The base of the flagellum of Ceromidae is similar to the small swelling, or basal peg (*Zapfen*), of the flagellum of *Karschia*. The field of short setae (prodorsal spiniform setal cluster, or *pdsc*) dorsal to the attachment point of the flagellum of Hexisopodidae resembles the setae at the base of the flagellum of Ceromidae. The narrow lumen in the scapus of the flagellum of Galeodidae bears some similarity to the flat apex of the flagellum of some Ceromidae. Alternatively, the flagellum of Galeodidae could be derived from that of Daesiidae, which also possesses a narrow lumen. Roewer (1934) concluded that the flagellum of Solpugidae is the most derived, and related to the flagellum of Daesiidae or that of Ceromidae based on similarities in the flagellar base.

Hewitt (1919b: 10), focusing only on southern African taxa, hypothesized a single origin of the flagellum, based on its putative derivation from a socketed bristle, which, it was argued, would imply that a rotatable flagellum is “more primitive” than the fixed flagellum of Solpugidae. Hewitt (1919b: 10) described the “primitive” flagellum of Daesiidae as a membrane with “more or less infolded edges,” which gave rise to the flagella of Ceromidae and Hexisopodidae by further infolding and extensive fusion along its length to form a flattened shaft. Hewitt (1919b: 10) also hypothesized that the bulbous base of the flagellum of Solpugidae is homologous with the “cuplike base” of *Blossia* (Daesiidae).

SINGLE OR MULTIPLE ORIGINS OF THE FLAGELLUM: The evidence supporting single vs. multiple origins of the male flagellum is summarized below. The potential for setae to be modified appears to be particularly strong among setae situated apically on the chelicera as evidenced by the wide array of setal forms associated with the flagellum of *Karschia* (pl. 30A–C). This may indicate that any of these setae could be a precursor to the flagellum, an argument for multiple origins. However, this wide array of setal modification is also consistent with a single origin of the flagellum, as it may explain how the diversity in flagellar forms could be derived from a similar original form, a possibility first suggested by Kraepelin (1908a: 223).

Positional homology of the attachment points of the flagellum on different parts of the fixed (dorsal) finger among taxa may appear to support multiple origins of the flagellum, e.g., the distally situated flagellum of Gylippinae (pl. 32H) versus the proximally situated flagellum of Hexisopodidae (pl. 32C). However, the diversity of cheliceral shapes is likely to affect not only where on the prolateral surface of the finger the flagellum is attached, but also how the teeth are distributed along its gnathal edge. When homologous teeth were used as landmarks for evaluating the position of the flagellum, flagella that appeared to be located in very different positions, were found to be aligned with the same landmark tooth (pl. 44). For example, the flagellum is attached dorsodistal on the finger in Solpugidae, medial in *Namibesia* (Daesiidae), and ventroproximal in Hexisopodidae. However, the points of flagellar attachment are approximately aligned with the fixed finger medial (FM) tooth in all three taxa and presumably shifted in association with changes in the shape of the chelicera. This example illustrates how apparent differences in the position of the flagellum do not necessarily contradict the criteria of positional homology. The hypothesis that the flagella of Hexisopodidae, Solpugidae, and *Namibesia* are homologous based on positional similarity is corroborated by their structural similarity.

If a homologous seta gives rise to the flagellum, in accordance with the hypothesis of a single origin thereof, the **flagellar attachment point** may be expected to retain the same position relative to other, less modified setae in the series from which the flagellum was derived. This does not appear to be the case, however, as noted also by Hewitt (1919b: 9), potentially supporting the hypothesis of multiple origins of the flagellum. On the other hand, variation in position of flagellar attachment, relative to the positions of other, less modified setae in the series from which the flagellum was derived is observed even among taxa in which the flagellum may reasonably be assumed to be homologous, e.g., within Solpugidae. For example, the point of flagellar attachment is approximately aligned with the apicalmost proventral distal (*pvd*) seta in *Zeria carli* (pl. 45A), the most common position in Solpugidae (Hewitt, 1919b: 11, fig. 1bC), but remote from the apicalmost *pvd* seta in *Oparba asiatica* (pl. 45D). Hewitt (1919b: 9) mentioned similar examples concerning differences in the relative positions of flagellar attachment points among species of *Blossia* (Daesiidae), but noted that the "original relation" to the row of *pvd* setae was retained, regardless of the differences. In the present study, the point of flagellar attachment in taxa with broad, membranous flagella, e.g., the bowl-, husk-, or vesicle-shaped flagella of Ammotrechidae, some Daesiidae (e.g., *Biton*), and Mummuciidae (pls. 136A, E, I, 146A, E, G, I) was usually further from the *pvd* series than in taxa with a stem or basally tapering flagellum, e.g., some *Blossia* and *Hemiblossia* (pl. 139C, G, I), suggesting a shift in attachment point relative to the *pvd* setae might be caused by the shape of the flagellum. Apparent differences in the position of flagellar attachment relative to the *pdd* and *pvd* setae may thus be unreliable indicators of flagellar homology.

FLAGELLAR PRECURSORS: Sørensen (1914: 177) observed that all modified spiniform setae situated dorsal to the flagellum, i.e., the flagellar complex subspiniform to spiniform (*fcs*) setae, are nonplumose, whereas all those situated proximal to the flagellum, e.g., the long plumose setae (flagellar complex plumose setae, or *fcp*) in *Karschia* (pls. 30A, 31A), or distal to it, e.g., the *fcp* seta/e in Solpugidae (pls. 45B; Sørensen, 1914: 212, fig. 10), are plumose. Sørensen (1914) thus concluded that the flagellum originated from the distalmost plumose seta or, in the case of Rhagodidae, the two distalmost plumose setae. Hewitt (1919b) agreed with Sørensen (1914), based on a study of developmental stages within Solpugidae: a three-malleoli stage juvenile, a subadult male, and an adult male *Solpugema derbiana* (Pocock, 1895). The juvenile possessed a single row of plumose setae ending in a distal nonplumose, slightly longer seta, whereas the subadult male possessed "several simple bristles of which one is markedly stouter than the rest and strongly curved like the feather bristles" near the distal end of the plumose series (Hewitt, 1919b: 11, fig. 1bA, B). Hewitt (1919b) concluded that the apicalmost of the plumose setae (proventral distal setae, or *pvd*) is the precursor to the flagellum of adult males, and referred to it as the "flagellar bristle." In the present study, a similar enlarged seta was observed in a subadult male *Metasolpuga picta* (pl. 46C), consistent with Hewitt's (1919b) observation that this seta is the precursor of the flagellum, at least in

Solpugidae. This unmodified seta is referred to here as the ventral flagellar seta (*vfs*). The *vfs* can thus be defined as the apicalmost seta in the proventral distal (*pvd*) series, usually also the apicalmost in the setose area of the fixed (dorsal) finger, and the seta on which both the *pdd* and *pvd* series converge (pl. 12, 47). The *vfs* is hypothesized to be the precursor of the primary (ventral) flagellum, and this is supported by the position of the flagellum relative to adjacent setae (pl. 46A, B). Directly dorsoproximal to the *vfs*, and belonging to the prodorsal distal (*pdd*) series based on its position, is the dorsal flagellar seta (*dfs*), which is hypothesized to be the precursor of the secondary (dorsal) flagellum of *Barrussus*, *Eusimonia*, and Rhagodidae. This differs from Sørensen's (1914) hypothesis that the seta ventral to *vfs* is the precursor of the ventral flagellum of *Barrussus*, *Eusimonia*, and Rhagodidae.

A broad survey of setation in female solifuges, based on 45 species representing all families, was undertaken during the present study, to investigate the differentiation and structure of the flagellar setae (*vfs* and *dfs*) across the order (pl. 47). The identity of the *vfs* as the apicalmost *pvd* seta was observed to be relatively obvious when the various prolateral series of setae (especially the *pvd* and *pdd* series) are well differentiated, e.g., in *Hemerotrecha branchi* Muma, 1951 (pl. 12), but not when apical setae on the finger are relatively homogeneous, e.g., in *Eremorhax joshui* (Brookhart and Muma, 1987) (pl. 72G). The *vfs* is nonplumose in Solpugidae (pl. 47C). In addition to its position relative to the *vfs* and *pdd* setae, a "typical" *dfs*, as in *Hemerotrecha branchi* (pl. 12), is pronounced in length, shape, and, often, girth (pl. 47A–C, E): it is usually the longest seta in the area, is gently recurved ventrally, and is often more robust than the other *pdd* setae. It is therefore readily identifiable except in the presence of an additional and similarly modified seta, the longest of which is often situated dorsal or dorsoproximal to the shorter of the two, which confused the identity of the *dfs* in a few species, especially among Daesiidae (pl. 47D). These cases are, however, irrelevant to the discussion of primary flagellar homology that pertains to the *vfs*, as proposed in the present contribution.

The position of the flagellar attachment point relative to the **proventral distal (*pvd*) setae** of Ceromidae and Galeodidae, and relative to the hypothesized prodorsal distal (*pdd*) setae of some Daesiidae may at first appear to contradict the hypothesis that the flagellum is derived from the apicalmost setae of the *pvd* series. The attachment point appears to be situated within the *pdd* series, not the *pvd* series in Galeodidae (pl. 59A, C, G), distal to, i.e., not aligned with, and partly obscured by several modified *pvd* setae (the flagellar complex plumose setae, or *fcp*) in Ceromidae (pl. 32A, B), and proximal to a regularly spaced row of what appear to be *pdd* setae in Daesiidae (pl. 34C). However, structures on the chelicera appear prone to shifts in position, and these examples could plausibly be explained by a shift in the flagellum relative to the *pdd* or *pvd* setae, or vice versa, allowing the point of flagellar attachment to remain next to the margin of the asetose area. Among the material examined during the present study, the male flagellum was, with one exception (Gylippinae), situated next to the margin of the asetose area of the fixed (dorsal) finger (e.g., pl. 4C), be it the prodorsal distal margin (pddm) or the proventral distal margin (pvdm), whereas the *pvd* and *pdd* setae were often found to be situated slightly more medioproximal on the chelicera when the flagellum was present. For example, in Galeodidae, the presence of one or two distinct plumose setae, morphologically most similar to the proventral distal (*pvd*) setae, situated proximoventral to the point of attachment of the flagellum and referred to here as the flagellar complex plumose (*fcp*) seta/e (pls. 4C, 30G, H, 61C), appears to locate the flagellum within the *pvd* series, but with the flagellum situated out of alignment and more dorsodistal toward the pddm. It is more parsimonious to hypothesize that the flagellum of galeodids shifted position, relative to the rest of the *pvd* series from which it was derived, than to hypothesize that it was derived from, e.g., the *pdd* series. Similar hypotheses may be advanced to account for the setae at the base of the flagella of Ceromidae and Daesiidae, or the apparent position of the *pvd* series and flagellum in the setiform flagellar complex (*sfc*) of Melanoblossiinae. Accordingly, observations of flagella situated out of alignment with the *pvd* and *pdd* setae do not falsify the hypothesis of primary homology of the flagellum.

Homology of the Flagellum

A single origin for the primary (ventral) flagellum of Solifugae is proposed here (see pl. 43 for summary). The hypothesis of primary homology is based on Remane's (1952) criteria of topographical and structural similarity, and intermediate forms, and builds upon the earlier hypotheses of flagellar homology by Kraepelin (1908a), Hewitt (1919b), and Roewer (1934: 135–155), augmented by an examination of specimens representing the diversity of flagellar morphology.

Composite Flagella: The modified *vfs* of the subadult *Metasolpuga picta* indicates that the *vfs* is the precursor of the primary flagellum of Solpugidae (pl. 46C). Structural similarity among the flagella of Solpugidae, Ceromidae, Hexisopodidae, and the daesiids *Namibesia* and *Syndaesia*, i.e., composite flagella comprising a stalk, base, and shaft, with the latter being predominantly chitinous, and usually whiplike, suggests that these flagella are homologous (pls. 32A–E, G, 43A–D). Similarity between the part of the flagellar shaft of Solpugidae that is fused to the fixed finger into a flagellar groove and the basal section of the membranous, straplike flagellum of Gylippinae that is also fused into a shallow groove suggests that the flagella of these families are also homologous (pls. 32F, 43F).

Males of the daesiid *Ammotrechelis* possess a unique flagellum (pls. 32F, 43E), which appears to represent a structurally intermediate form between the whiplike flagella of the taxa discussed above (Ceromidae, Gylippinae, Hexisopodidae, Solpugidae, and the daesiids, *Namibesia* and *Syndaesia*), and the membranous bowl-shaped flagella of, e.g., Ammotrechidae (pls. 34E, F, 43H). The flagellum of *Ammotrechelis* comprises two distinct components. An elongated shaft resembles the shafts of the whiplike flagella, including the presence of a hemolymph lumen and an alembic lumen. The base is broad and membranous, however, resembling the membranous bowl-shaped flagellum of Ammotrechidae. The latter, in turn, is similar to the membranous flagella of most Daesiidae (i.e., excluding *Namibesia* and *Syndaesia*), and Mummuciidae (pls. 34A–D, G, H, 43G, I). Based on these structural similarities, the flagellar base of *Ammotrechelis* is therefore hypothesized to be homologous with the bowl-, husk-, or vesicle-shaped membranous flagella of Ammotrechidae, most Daesiidae, and Mummuciidae, while the shaft is hypothesized to be homologous to the shaft of Ceromidae, Gylippinae, Hexisopodidae, Solpugidae, and the daesiids, *Namibesia* and *Syndaesia*. The hypothesis that the shaft is homologous to the whiplike flagella is independently supported by new evidence of a possible phylogenetic relationship between *Ammotrechelis* and *Syndaesia*, i.e., the retrolateral granular tubercle and the bifurcated movable finger medial (MM) tooth (cf. pl. 134B, D in the present contribution and fig. 3 of Maury, 1985: 5). The probable homology of the flagellar base of *Ammotrechelis* and the membranous flagellum of most Daesiidae is further supported by the similar hairpin-shaped transition of the short stalk into the flagellar base (pl. 40 G–I) as well as a prodorsal crossover within the dorsal margin of the flagellum (pl. 40G, I, arrows) in these taxa. The flagellum of *Ammotrechelis* implies that the base of the chitinous whiplike flagellum is homologous with the membranous bowl-, husk-, or vesicle-shaped flagella.

Sessile (Primary and Secondary) Flagella: The sessile flagellum of the karschiid, *Karschia* (pls. 30A, 40C) shares structural and positional similarities, indicative of homology, with the composite flagella (pl. 43J). Structural similarities include its filiform character and the swelling at its "base," which resembles the base of the whiplike flagella, as suggested by Roewer (1934) in his comparison of *Karschia* and Ceromidae. The distalmost (or dorsalmost) position of the flagellum of *Karschia*, relative to the *pvd* setae, strongly supports its derivation from the apicalmost *pvd* seta, i.e., the *vfs*, from which the composite flagellum is also proposed to derive. The flagella of *Karschia* and *Dinorhax* share structural similarities, implying homology, e.g., both are long and filiform, and appear to have been modified longitudinally as indicated by a longitudinal plumose fringe on the flagellum of *Karschia* (pls. 30A, 31A) and a longitudinal sulcus in the flagellum of *Dinorhax* (pls. 30E, 41A). The flagellum of *Karschia* also shares positional and structural similarities with the sessile flagella of *Barrussus*, *Eusimonia*, Galeodidae, and Rhagodidae, i.e., a similar origin relative to the proventral distal (*pvd*) setae and probable prodorsal distal (*pdd*) setae, as in Rhagodidae, *Eusimonia*, and probably *Barrussus*, a deep socket (alveolus) as in Galeodidae and Rhagodidae, and a distinct elevation on the socket margin (**socket margin elevation**, or **sme**), as in Galeodidae, Rhagodidae, and *Eusimonia* (pls. 30B, D, F, H; 40A, B, C).

Positional similarities are also evident between the flagellum and adjacent dorsal and ventral setae of *Dinorhax* (pl. 30E, 43N) and the flagellar complex of some other taxa, especially Eremobatidae (pls. 38, 39, 46A). In both taxa, the flagellum is situated distally on the fixed (dorsal) finger, the associated modified setae inserted directly dorsoproximal and ventroproximal to it, and the flagellum originates from a similar elevated socket. Two sources of evidence therefore support the hypothesis that the flagellum of *Dinorhax* is homologous with the flagella of *Karschia* and Eremobatidae and, by extension, the flagella of all other taxa with which these are homologous.

Two groups of Solifugae, i.e., Rhagodidae and the karschiid genera, *Barrussus* and *Eusimonia*, possess two distinct flagella, the ventral and dorsal flagellar structures referred to, respectively, as the primary and secondary flagella (pls. 30D, F, 31B, D). A third karschiid genus, *Barrus*, apparently possesses a single flagellum (Roewer, 1934: 305, fig. 227A), whose structure implies homology with the secondary flagellum of the other three taxa. The flagella are fairly stable in structure and position of attachment in *Eusimonia* and especially Rhagodidae. The primary flagellum of most *Barrussus* and *Eusimonia* resembles that of Rhagodidae in structure and position (pls. 30D, F, 31B, D). The attachment points of the primary flagella of Rhagodidae, *Barrussus*, and *Eusimonia* are aligned with and situated at the distal end of the row of *pvd* setae, suggesting they developed from the *vfs* and are therefore homologous to the whiplike flagella of Ceromidae, Gylippinae, Hexisopodidae, Solpugidae, and the daesiids, *Namibesia* and *Syndaesia*, and thus also to the membranous bowl-, husk-, or vesicle-shaped flagella of Ammotrechidae, other Daesiidae, and Mummuciidae. The secondary flagellum, situated directly dorsal to the primary flagellum, is thus likely derived from the *dfs*, and therefore assumed to be homologous in *Barrussus*, *Eusimonia*, and Rhagodidae based on their similar positions, and also in *Barrus* based on structural similarity to the secondary flagellum of the other two previously mentioned karschiid genera.

The flagellum of Galeodidae (pls. 30G, H, 31E, F, 43M) is more dorsoproximally situated than the flagella of other solifuge taxa, but the presence of one or two distinct plumose (*fcp*) setae at its point of attachment suggests a dorsoproximal shift in the *pvd* series (see section on Flagellar Precursors), implying that the flagellum of Galeodidae is derived from the *vfs*, and thus homologous to the primary flagellum of Rhagodidae, *Barrussus*, and *Eusimonia*, as well as the whiplike and membranous bowl-, husk-, or vesicle-shaped flagella of the other taxa discussed previously.

An alternative hypothesis concerning the homology of the sessile flagella of *Barrussus*, *Eusimonia*, Galeodidae, and Rhagodidae may be considered, however. A curved, elevated socket margin (socket margin elevation, or sme) of striking similarity is evident at the proximal or dorso- to ventroproximal margin of the socket of the (primary) flagellum of *Karschia*, the secondary (dorsal) flagellum of Rhagodidae, the primary (ventral) flagellum of *Eusimonia* and probably *Barrussus*, and the flagellum of Galeodidae (pls. 30B, D, F, H; 40A–C). If this feature were homologous in all four taxa, it might imply that the dorsal flagellum of Rhagodidae, the ventral flagellum of *Barrussus* and *Eusimonia*, and the flagella of Galeodidae and *Karschia* are homologous to the primary flagellum, thus leaving the ventral flagellum of Rhagodidae without a flagellar homolog in solifuges, while the dorsal flagella of *Barrussus* and *Eusimonia* remain homologous to secondary flagella. On the other hand, however, the sockets of the primary and secondary flagella may have fused, shifting the socket margin elevation (sme) to the dorsal position it occupies near the secondary (dorsal) flagellum of Rhagodidae. This possibility is supported by the structural similarity of the alveolus, the deep depression into which the flagellum/a is/are attached in Galeodidae, *Karschia*, and Rhagodidae. Pending evidence to the contrary, therefore, the flagellum of Galeodidae is considered homologous to the flagellum of *Karschia* and the primary (ventral) flagellum of *Barrussus*, *Eusimonia*, and Rhagodidae, in accordance with the hypothesis initially proposed in the present contribution.

Setiform Flagella: The setiform structures traditionally referred to as flagella in Eremobatidae and Melanoblossiinae, which always form part of a **setiform flagellar complex (*sfc*)**, are probably independently derived. The flagellum of Eremobatidae is clearly derived from the *vfs* (e.g., pl. 46A), indicating its homology with the primary flagellum of the order. Similarities between the flagella of Eremobatidae and *Dinorhax* were mentioned earlier. The flagellar groove of Eremobatidae (e.g., Brookhart and Muma, 1981: 291, figs. 2, 3) resembles that of Mummuciidae (e.g., Botero-Trujillo, 2014: 325, figs. 13, 15), both being demarcated by strong borders and opening toward the distal end of the fixed (dorsal) finger. The position of flagellar attachment, relative to the groove, is also similar in these taxa, although this may be due to convergence, the flagellum emerging close to the base of the groove that protects it.

It is more challenging to identify the flagellum of Melanoblossiinae (pl. 36G, I) and homologize it with other primary flagella. The setiform flagellar complex (*sfc*) of Melanoblossiinae is greatly modified, obscuring the underlying pattern of the *pvd* series, which appears to have shifted markedly such that the flagellum is not situated distally in the *sfc*, but nonetheless distally in the distalmost row of setae, i.e., what appears to be the ventralmost row of *pvd* setae on the fixed finger of the unmodified chelicera of juveniles, subadults and females.

The problem is complicated further by the discovery that the most obviously modified setae, in *Lawrencega* (“a” in pl. 36G) and *Melanoblossia* (“b” in pl. 36G, I), are not homologous. An undescribed *Melanoblossia* species examined in the present study possesses a typical *Melanoblossia* type of *sfc*, with homologs of both the modified *L. procera* seta (“a”) and the modified *M. braunsi* seta (“b”) distinctly differentiated and prominent (pl. 26, 36I). In this species, the seta with limited plumosity (“a” in pl. 36I) is the distalmost seta in a short row of setae inserted below a row of strongly plumose setae situated proximally within the *sfc*. Based on its distalmost position in the putative distal row of modified *pvd* setae, seta “a” is hypothesized to be derived from the *vfs*, and therefore homologous to the primary flagellum of the order. Although only slightly differentiated from the other setae in its row, the flagellum is prominent and slightly longer than the other *sfc* setae (fig. 26).

The setiform flagellar complex principal seta (*sfc principal seta*) (“b”), rather than the flagellum (“a”), is usually the most prominent seta in the *sfc* of *Melanoblossia*, and is traditionally interpreted as the flagellum (e.g., Purcell, 1903a: 6). Assuming that this seta is homologous to the secondary flagellum of Rhagodidae, *Barrussus* and *Eusimonia* would imply a major ventral shift of the dorsal flagellar seta (*dfs*), established above to be derived from the *pdd* series, to a position separated from the other *pdd* setae, and aligned with the setae more parsimoniously interpreted as a modified second *pvd* row. It is therefore more plausible to conclude that the *sfc principal seta* is a modified *pvd* seta, situated in a more proximal row of the series.

Flagellum of *Xenotrecha huebneri*: Kraepelin (1908a) hypothesized that the flagellum of Solpugidae comprises two setae fused into a single structure. The single differentiated seta, i.e., the *vfs*, of the subadult male *Metasolpuga* Roewer, 1934, regarded here as the precursor of the flagellum (pl. 46C), does not support Kraepelin's (1908a) hypothesis for the origin of the flagellum of Solpugidae, however. The only example of a flagellum that could potentially comprise two fused setae is that described for *Xenotrecha huebneri* (Kraepelin, 1899). Maury (1982: 137, fig. 22, 27, 28) described and illustrated a plumose seta arising from near the center of the flagellum of *X. huebneri*, and extending almost to its tip. This seta was described as similar to the *pvd* setae, although it appears to possess a broad base in the illustrations of Maury (1982: 137, fig. 22, 27, 28). A configuration in which a seta perforates the base of the broad membranous flagellum might be the precursor for a transitional type of flagellum as in *Ammotrechelis*. The male of *X. huebneri* is, however, known only from a single specimen and the possibility that its flagellum is abnormal cannot be disregarded. The most parsimonious hypothesis remains a single setal origin for the primary flagellum, as discussed above.

Flagellar Complex

The male flagellum is often associated with various modified spiniform and setiform setae. These include the **flagellar complex subspiniform to spiniform (*fcs*) setae**, i.e., the one to four spiniform setae situated near the point of attachment of the flagellum of Ceromidae (pl. 93A–C), Galeodidae (pl. 63A, D), Karschiidae (pls. 51B, 55A), and Gylippinae (pl. 86A), the **flagellar complex plumose (*fcp*) setae**, i.e., the suite of variously modified setae situated ventral to the flagellum of *Karschia* (pl. 51A), the one or two plumose setae situated proximoventral to the point of attachment of the flagellum of Galeodidae (pl. 63A, D), the often pipette-shaped *pvd* setae arranged in a row at the base of the flagellum of Ceromidae (pl. 93A, C), and the robust retrolateral manus spiniform (*rlms*) seta of Gylippinae (pls. 85B, 86A, B, D). This combination of modified setae constitutes the flagellar complex of a male solifuge.

The subspiniform to spiniform (*fcs*) setae of Ceromidae, Galeodidae, Gylippinae, and Karschiidae are invariably situated dorsally. Although the dorsal position obscures their origin, their location relative to the flagellum and the prodorsal distal margin (pddm) of the fixed finger asetose area suggests that they are probably modified *pdd* setae (pls. 30A–D, G, H, 32B, H,). One to four *fcs* setae appear to originate proximal to the flagellum next to the margin of the asetose area in galeodids (pls. 4C, 30G, H). The relative positions of these setae are similar in *Ceroma* (pl. 32B). The positions of the robust *fcs* setae of *Gylippus* (pl. 32H) are, in turn, similar to the *fcs* setae of *Ceroma*, suggesting that the *fcs* setae of Ceromidae, Galeodidae, and Gylippinae are homologous. The subspiniform (*fcs*) setae of *Karschia* (pl. 30A) are situated directly dorsoproximal to the flagellum, resembling the position of the dorsal flagellar seta (*dfs*) relative to the ventral flagellar seta (*vfs*). Although the *fcs* setae are more dorsally situated in *Eusimonia* (pl. 30D) than in *Karschia* (pl. 30A), these setae are probably homologous given the frequency with which structures shift on the chelicera and the putatively close phylogenetic relationship between the two genera.

The flagellar complex plumose (*fcp*) setae, as defined here, are hypothesized to be modified proventral distal (*pvd*) setae, hence the term "plumose" in reference to the plumose nature of unmodified *pvd* setae. Although the *fcp* setae are nearly always plumose, exceptions exist, e.g., the *fcp* setae of some ceromids, the plumosity of which is vestigial to absent, having probably been lost secondarily. The flagellar complex of *Karschia* includes highly modified *pvd* setae, the *Säbelborsten* of Kraepelin (1908a: 222), which become increasingly modified distally (30A, 31A). A row of *pvd* setae, often pipette-shaped and smooth or plumose, inserted at the base of the flagellum (pls. 32A, B, 33A–C), may constitute a synapomorphy for Ceromidae (excluding *Toreus*). The presence of one (usually) or two stout, plumose setae situated directly proximoventral to the point of attachment of the flagellum (*fcp* in pl. 30G, H; Birula, 1936a: 48, fig., 1937a, 1937b, 1938; Panouse, 1960b: 178, fig. 4) is a potential synapomorphy for Galeodidae. Although not obviously connected to the *pvd* row, these setae appear to be homologous with the *pvd* setae based on their structure and position relative to the rest of the *pvd* setae.

The **setiform flagellar complex (*sfc*)** of Eremobatidae, Lipophaginae, and Melanoblossiinae differs fundamentally from the flagellar complexes of other taxa, which comprise a distinct flagellum associated with well differentiated, modified setiform and spiniform setae, in that the *sfc* comprises a cluster of slightly to markedly modified setae, all of which, including the flagellum if present, are setiform.

The **type A setiform flagellar complex (*type A sfc*)** of eremobatids (pls. 37–39; tables 15, 17) usually comprises modified *pdd* setae (pl. 37D), which may be striated or weakly plumose, with or without modified proventral distal (*pvd*) setae, and sometimes modified promedial (*pm*) and proventral subdistal (*pvsd*) setae, but never consists entirely of modified *pvd* setae. The *sfc* may be a heterogeneous (e.g., in *Eremobates*, pl. 38A) or relatively homogeneous (e.g., in *Chanbria*, pl. 37A) cluster of setae (table 15, 17), but its extent is always ill defined. A flagellum may be absent or present and, if present, is always setiform and partly or entirely obscured by the other *sfc* setae. Setae in the *type A sfc* are closely associated with the fixed finger, converging or arranged along it.

A flagellum is absent in the **type B setiform flagellar complex (*type B sfc*)** of Lipophaginae (pl. 36A–F) and all setae in the *sfc* tend to be similarly modified *pvd* setae, e.g., in *Lipophaga trispinosa* (pl. 36B), or two types of similarly modified *pvd* setae in *Bdellophaga angulata* (pl. 36D–F). Setae forming the *type B sfc* are usually clearly identifiable as part thereof, distally directed, irrespective of the shape of the fixed finger, and may extend well beyond the boundaries of the fixed finger as in *Bdellophaga angulata*. However, the extent of differentiation of the apical prolateral setae, especially the *pvd* setae on the fixed finger of *Trichotoma michaelseni,* is so minor that a *type B sfc* is considered absent in this species.

The **type C setiform flagellar complex (*type C sfc*)** of Melanoblossiinae (fig. 26, pl. 36G–I) consists entirely of *pvd* setae, like the *type B sfc* of Lipophaginae. A setiform flagellum is weakly differentiated, and its presence in different melanoblossiine species needs to be verified. The *type C sfc* is unique in various ways. Firstly, a distinct setiform flagellar complex principal seta (*sfc principal seta*), often more prominent than the flagellum itself, if present, is the dorsalmost seta in the *sfc*. Secondly, setae of the *sfc* are arranged in a compact cluster forming a well-defined unit. Lastly, the setae forming the *sfc* are situated in a broad, shallow depression, referred to here as the flagellar complex depression (cf. the flagellar groove, which accommodates the flagellum in several other taxa), fully protected by the finger, which forms a convex ventral enlargement, the medioventral excrescence (MVE) to accommodate the *sfc* (fig. 26, pl, 159).

The setiform flagellar complexes of Eremobatidae (*type A sfc*), Lipophaginae (*type B sfc*), and Melanoblossiinae (*type C sfc*) share few similarities. According to the interpretation proposed here, the *type B* and *type C sfc*, both comprised entirely of *pvd* setae, are homologous to the **setiform flagellar complex (*sfc*) ventral series** (pl. 38A, B) of the *type A sfc*, characteristic of eremobatids such as *Eremobates.* Unlike the *type B* and *type C sfc*, no eremobatid *type A sfc* was found to be entirely comprised of *pvd* setae. The *type B* and *type C sfc* may be homologous, but differ greatly in the arrangement and structure of their individual setae.

Except for the *type B* and type *C sfc*, derived from *pvd* setae, and the primary flagellum of various taxa derived from the ventral flagellar seta (*vfs*) that belongs to the *pvd* series, the most commonly modified setae, and those with the most pronounced modifications, are the prodorsal distal (*pdd*) series. Examples include the subspiniform *pdd* setae of some *Hemerotrecha* (e.g., pl. 37D) and the flagellar complex subspiniform to spiniform (*fcs*) setae of Ceromidae, Galeodidae, Gylippinae, and Karschiidae. Contrary to Sørensen's (1914: 177) initial assessment, the *pdd* setae may also be plumose, as in *Dinorhax* (pl. 30E), although this is uncommon. Plumosity is therefore not necessarily restricted to the proventral distal (*pvd*) setae.

Absence of the Flagellum

The absence of definitions for the flagellum and the flagellar complex has created confusion regarding whether a flagellum is present in all male solifuges. For example, a flagellum has been reported to be present in all known species (e.g., Lamoral, 1975), in most species (Hewitt, 1919b), or in all except Eremobatidae (e.g., Punzo, 1998a; Dunlop et al., 2004; Bayram et al., 2011). In character 34 of their morphological data matrix, Pepato et al. (2010) coded the flagellum present in *Chanbria*, the known species of which do not possess a flagellum as defined here, and absent in *Eremobates*, in which a flagellum is present.

Most of the confusion concerns Eremobatidae. There is a mistaken perception that eremobatids are unique among Solifugae in lacking a flagellum (Kraepelin, 1901: 6, but not Kraepelin, 1908a: 223; Punzo, 1998a; Bayram et al., 2011) or having the flagellum replaced by a suite of modified setae, i.e., a flagellar complex (e.g., Klann, 2009). Rocha (2002: 441) stated that "the most distinctive shape of the flagellum is present in Eremobatidae, the only family with hairy flagella [which] consist of a complex of modified bristles." Statements such as these are misleading. Firstly, a distinctly modified seta that satisfies the definition of a flagellum may be present, as in *Eremobates* (pls. 38, 39A–F), or absent, as in *Eremocosta* (pls. 37C, 39G–J), both in family Eremobatidae. Secondly, the setal flagellar complex (*sfc*) is formed by relatively undifferentiated setae, without a flagellum, in some Eremobatidae, e.g., in *Eremocosta titania* (Muma, 1951) (pls. 37C, 39I), similar to that in the lipophagine *Trichotoma michaelseni* (pl. 36A), with the *sfc* best described as absent or near absent in both. Previous references to "flagellar complex" instead of "flagellum" are more descriptive of the suite of modified setae in eremobatids. However, the use of "flagellar complex" to refer to the flagellum and all modified setae associated with it in Ceromidae, Karschiidae, and Melanoblossiinae (Roewer, 1934: 144; 1941: 117, 127; Pieper, 1977) does not differentiate the eremobatid flagellar complex from these examples. The term setal flagellar complex (*sfc*) was introduced here to refer to the cluster of modified setae in Eremobatidae (*type A sfc*), Lipophaginae (*type B sfc*), and Melanoblossiinae (*type C sfc*), which may (some Eremobatidae and some Melanoblossiinae) or may not (Lipophaginae, some Eremobatidae, and some Melanoblossiidae) possess a flagellum as part of the flagellar complex.

By defining the flagellum in terms of setal modification, the presence of a flagellum becomes a character state of "ventral flagellar seta (*vfs*) modified and differentiated from surrounding setae," as opposed to "*vfs* unmodified," which would apply to females and immature males, or "*vfs* modified similarly to surrounding setae," which would apply, e.g., to Lipophaginae.

In addition to the suprageneric taxa in which a flagellum is absent (Lipophaginae, some Eremobatidae, and some Melanoblossiinae), a few other, mostly monotypic genera belonging to families in which a distinct flagellum is usually present, were diagnosed partly or entirely on the absence of a flagellum. Examples are *Toreus* (Ceromidae), *Microblossia* (Melanoblossiinae), *Siloanea* (Hexisopodidae), and *Rhinippus* Werner, 1905 (Karschiidae). The validity of several of these genera was later questioned, and some were synonymized. *Rhinippus* was based on the absence of a flagellum (Werner, 1905) but synonymized with *Barrussus* after Roewer (1934) recognized a flagellum in the type. In the other cases, the identification of the type specimens as adult males was called into question (e.g., *Siloanea*) or the species was considered a potential transitional form between taxa (e.g., *Microblossia*). *Siloanea* was synonymized with *Chelypus* by Wharton, 1981, while Lawrence (1962b) questioned the sex of *Toreus* (Ceromidae). If the holotype of *Toreus* is indeed male, this species might be more closely related to Lipophaginae, in which the flagellum is absent, rather than Ceromidae. Similarly, for *Microblossia* (Melanoblossiinae), Wharton (1981: 60) mentioned that "if the holotype...is actually an adult male, a detailed examination of the specimen should reveal relationships between Melanoblossiidae and other solifuge families." However, both *Toreus* and *Microblossia* are known only from the holotypes. More material, including series containing both sexes, is needed to resolve these questions.

Finally, Warren (1939) reported the absence of a flagellum in apparently abnormal adult males of the family Solpugidae. These males possessed a swollen opisthosoma, giving the appearance of gravid females. Despite the absence of a flagellum, the reproductive organs were clearly male, albeit "represented by the merest rudiments," and their genital plates (opercula) remained "in a more or less juvenile condition" (Warren, 1939: 140, 141). According to Warren (1939) the incidence of this condition, referred to as gigantism, was relatively high in the two populations examined (20% in *Solpugema hostilis* White, 1846 and 13% in *Solpuga chelicornis*). Warren (1939) considered the possibility of parasitism as a causal factor, but found no evidence thereof. No further reference to this or any similar abnormality was encountered during the present study.

Flagellar Variation and Taxonomic Significance

The flagellum plays an important role in the taxonomy of Solpugidae at the species level. However, an apparently limited amount of variation among what were assumed to be closely related species prompted Hewitt (1919b) to suggest that the flagellum is of little value at the generic level. Considering that many solpugid genera may not be monophyletic, Hewitt's (1919b) opinion may be misleading.

Few data are available concerning intraspecific variation in aspects of the solifuge flagellum. Wharton (1981: 52) reported "considerable variation" in the shape of the cuplike flagellar base of *Hexisopus pusillus*. The morphologically uniform group of large nocturnal southern African *Zeria* species with a long flagellar shaft are distinguished largely on the basis of the relative length of the shaft and microstructures thereon (Hewitt, 1919b; Wharton, 1981). These characters, sometimes representing minor differences such as the shape of the tip of the shaft, e.g., in *Z. obliqua* (Roewer, 1933), or a paler area subapically on the shaft, e.g., in Namibian *Z. monteiri* (Pocock, 1895), are often corroborated by dentition and geographical distribution, thus providing some basis for the stability observed in flagellar morphology at the species level. Wharton (1981) presented a detailed investigation of intraspecific variation in the flagellar shaft of a series of *Metasolpuga picta*. Subapical denticles (serrations) on the shaft varied in the level of differentiation, from fairly distinct to absent. Wharton (1981) speculated that variation in curvature of the shaft near its base might be related to the male's mating history. Of particular interest is a negative correlation between the size of the male and the relative length of its flagellum.

The general absence of revisionary studies on solifuges seldom permits evaluation of intraspecific variation, especially regarding geographically widespread species. For example, Purcell (1899) reported variation in flagellar length of more than

1.3 times the width of the ocular tubercle for specimens of the widely distributed *Zeria venator* from different localities. Purcell (1899) found no reliable character by means of which the species might be subdivided, but Hewitt (1919b: 13) noted that this range in flagellar length might indicate "several races or local forms" if intermediate forms proved to be absent. Hewitt (1934: 404) reported variation in the "slenderness of the flagellum" of *Blossia falcifera*, coincident with variation in other characters such as the relative length of the mucron. Wharton (1981) pointed out that Lawrence (1928, 1953, 1959, 1961) described several species and subspecies of *Solpugassa* based on flagellar proportions. Wharton (1981) argued that these characters might be allometric, noting the presence of minute spicules on the forks at the tip of the shafts in all specimens examined, and emphasized the need for more specimens to study flagellar variation within and among populations. Hewitt (1919b: 13) mentioned that the tip of the flagellum of *Solugema hostilis* is "quite constant," but variable in *S. derbiana* and therefore cannot be used "as an absolute unit character."

Interspecific similarity in flagellar morphology concerning the sharp, bladelike tip of the flagellum in various species of *Solpuga* now mostly placed in *Solpugema*, i.e., *Solpugema derbiana*, *S. hamata*, *S. hostilis*, *S. tookei* (Hewitt, 1919), and *Solpuga bechuanica* Hewitt, 1914, was noted by Hewitt (1919b: 14). Such interspecific similarity in flagellar morphology might be indicative of monophyletic groups. As with dentition, however, the lack of a robust systematic framework hampers evaluation of the value of flagella in solifuge taxonomy at the species or generic levels.

Structures associated with the flagellum should also be evaluated for variation. For example, Brookhart and Muma (1981: 287) reported that variation in the "mesoventral groove and [its] basal flange [was] subtle but consistent... among populations" of the *pallipes* group of *Eremobates*.

Functional Morphology of the Flagellum

The precise functions of the flagellum remain elusive. Earlier speculated to be a sensory seta (Bernard, 1896), it has since been shown that no nerves are associated with the flagellum of Solpugidae (Lamoral, 1975). Warren (1939) proposed that the flagellum is used to stimulate the female. Heymons (1902) and Junqua (1962) observed that copulation was unaffected when the flagellum was removed in two species of Galeodidae (whether these copulations resulted in fertilized eggs is unknown, however), prompting some workers (e.g., Cloudsley-Thompson, 1961; Lawrence, 1963) to state that the flagellum plays little or no role in reproductive success. On the other hand, Sørensen (1914: 170) stated that the flagellum is unquestionably a copulatory organ developed to collect (*Rhagodes*) or retain (*Galeodes*, *Solpuga*) seminal fluid, i.e., *une masse visquese*. To date, its function as an organ that holds sperm proved true only for the bowl-shaped flagellum of the ammotrechid *Oltacola chacoensis* (vide Peretti and Willemart, 2007). Only three observations support the hypothesis that the flagellum has some function during copulation itself, although the details appear to differ among taxa (table 2).

A possible mechanical function of the flagellum is likely facilitated by hemolymph action. Despite the great diversity in flagellar morphology (e.g., pls. 30–40), all flagella are either inserted into the chelicera in a distally directed position, as in Ammotrechidae, Eremobatidae, Gylippinae, Rhagodidae, Melanoblossiinae, Mummuciidae, and the karschiid genera, *Barrus*, *Barrussus*, and *Eusimonia*, or are able, probably by means of hemolymph pressure, to be directed distally by rotation in the socket, as in Ceromidae, Daesiidae, Galeodidae, and Hexisopodidae, by projection of the flagellum, as in Solpugidae, or by rotation and extension as in the karschiid genus, *Karschia*. This commonality was first noted by Sørensen (1914: 165), who identified a section of weakly sclerotized cuticle at the base of the flagellum of some solpugids, where the flagellum "articulates" during forward movement. In the present study, this apparently weaker cuticle was confirmed in Solpugidae (pl. 49A, B, arrows), the only family to possess a proximally directed flagellum that is fixed to the chelicera but able to be distally directed, again presumably by means of hemolymph pressure. A distally directed flagellum would place the flagellum, and particularly its apex, closer to and deeper into the female reproductive tract when inserted during the female genital contact phase (table 2). Hemolymph pressure might also improve the function of a membranous flagellum as an intromittent organ by increasing its rigidity, and hence its ability to retain and transfer sperm. The flagellum may also assist movement of the aflagellate spermatozoa of solifuges (Klann et al., 2009) by inducing, through an as yet unknown mechanism, the muscles around the female reproductive tract to move the spermatozoa along. Strong muscles surrounding the female reproductive tract were observed in a galeodid studied by Klann (2009: 164), suggesting mechanical displacement of sperm within the female genital system. The flagellum may also function to break up the sheath surrounding individual spermatozoa or groups thereof in some taxa. Among seven families studied by Klann et al. (2009, 2011), viz. Ammotrechidae, Daesiidae, Eremobatidae, Galeodidae, Hexisopodidae, Karschiidae, and Solpugidae, only Eremobatidae and Solpugidae were reported to possess separate, nonbound spermatozoa that do not need to be freed from a cluster, package, or surrounding sheath prior to fertilization, suggesting that the type of sperm packaging possessed by a solifuge taxon may be related to its flagellar morphology (table 3). It should, however, be noted that the presence of a sperm droplet, as opposed to a sperm packet, e.g., a spermatophore, might appear to conflict with field observations (Wharton, 1987), as it may not be possible for a male to pick up a nonbound sperm droplet and insert it into the female genital aperture. Conversely, a viscous droplet, bound by surface tension, may suffice.

The diversity in flagellar morphology may indicate different taxon-specific functions. For example, the uniform diploflagellum of different species of Rhagodidae (pl. 30F), and probably also the largely similar flagella of different species of Ammotrechidae (pl. 34E, F) and Galeodidae (pl. 30G), suggest a general functionality for the flagellum, which may or may not be in addition to species-specific functions. For example, the ubiquitous bowl shape of the flagellum among different species of Ammotrechidae suggests a general function for sperm retention and transfer, as confirmed in one species of Ammotrechidae (Peretti and Willemart, 2007), whereas species-specific variation in the shape of the apex, e.g., truncated to spouted (pl. 34E, F), suggests a function in specific-mate recognition or sexual selection through cryptic female choice.

Species-specific modifications to the flagellum of Solpugidae typically involve microstructures (denticles, hooks, lamellae, etc.), concentrated on the distal part of the flagellar shaft (pl. 49), which present the greatest diversity in form and position among the flagella of the family. The only area in which these microstructures come into sufficiently close contact with the female during mating is in her reproductive tract (table 2). The female reproductive system comprises two ovaries, each connected to a relatively short oviduct, which open into a single genital chamber, variously referred to as the copulatory pocket or seminal reservoir (Dufour, 1861: 434), the "uterus and vagina" (Birula, 1892), or the "genital vestibule" (Warren, 1939), connected to the exterior via a gonopore situated on the second abdominal segment (see Klann, 2009: 141, fig. 84B). The lumen of the genital chamber is lined with a thick but flexible, chitinous layer (Warren, 1939; Vachon, 1945; Klann, 2009). Subdivision of the oviduct of Solpugidae into the oviduct proper and the oviducal chamber (Warren, 1939) may be relevant to the shape of the flagellum in this family. After passing through the oviduct proper with its thick lining of chitin, the long whiplike flagellum likely enters the oviducal chamber through a very narrow duct that bends back upon itself before entering the chamber, as illustrated by Warren (1939: 143, fig. 2d), bringing the distal part of the flagellar shaft, with its species-specific microstructures very close to the sides of the duct. The most likely area for species-specific mate recognition or cryptic female choice may therefore be the part of the female oviduct that connects with the oviducal chamber. Similar female reproductive tract anatomy may exist in other taxa with long whiplike flagella, but no data are available. It is noteworthy, however, that denticlelike microstructures on the whiplike flagellum of Hexisopodidae are weakly developed or absent, suggesting that the whiplike flagellum might fulfill at least partly different functions in different taxa.

Two canals (or lumens) are present in the whiplike flagellum of Solpugidae (pl. 41A; Lamoral, 1975), Ceromidae (pl. 41K–N), Hexisopodidae (pl.41F–J), and the daesiid genera *Ammotrechelis* (pl. 32F), *Namibesia* (pl. 32E), and most likely also *Syndaesia*. Whereas the hemolymph lumen is closed to the exterior, the alembic lumen opens to the exterior at the flagellar apex, suggesting a possible exocrine function for the alembic fluid. Lamoral (1975) hypothesized that the secretion serves as a pheromone, but this is unlikely if it is excreted within the female reproductive tract, as indicated by circumstantial evidence, at least for Solpugidae. For example, a glistening at the apex of the flagellum of a male *Metasolpuga picta*, when withdrawn from the female genitalia (R.A. Wharton, personal obs.) suggests that secretion occurred during insemination or postinsemination genital chewing (alternatively, the glistening substance represents the remnants of seminal fluid). In these observations, the only such observations involving a whiplike flagellum, the entire shaft was inserted into the female (R.A. Wharton, personal obs.). The flagellum of *M. picta* is almost the length of its chelicera (pl. 97B) and can thus be inserted deep into the female genital tract, most likely extending along the oviduct proper and into the oviducal chamber (table 4) where it may secrete the alembic fluid. The thick cuticular lining of the oviduct proper would protect it from being ruptured by the sclerotized male flagellum during insertion. Dirt, which is often observed in the alembic lumen, sometimes far down the shaft, may have entered after the alembic fluid was dispelled, indicating that the male has mated. More data are needed to shed light on the functional morphology of the flagellum, including measurements (different aspects of the flagellar shaft, depth of shaft insertion, length of different parts of the female reproductive tract), comparative reproductive tract morphology (representative of different flagellar types), sperm morphology, and additional observations of mating behavior in a range of taxa.

The function of the plumose (*fcp*) setae and subspiniform to spiniform (*fcs*) setae associated with the flagellum of some taxa (e.g., pl. 30A-D, G, H, 32B, H), as well as additional processes and flanges on the male chelicera (e.g., pl. 20), especially apically, are unknown, but, given their diversity across the order, are most likely sexually selected (Hewitt, 1919b: 15).

Modified setae in the setiform flagellar complex (*sfc*) of Eremobatidae may function to detect the presence of and/or remove sperm from a previous mating. Indeed, remnants of seminal fluid were observed on the fingers of males postmating (Muma, 1966b). According to Muma (1966b), copulation among eremobatids is complete only after the male chelicera has made contact with a seminal globule, which is supported by the observation of an aberrant mating in which a male mounted a female 50 times in the course of 40 minutes, in an endless loop of "sperm transfer" and genital prodding until the pair were separated. Muma (1966b: 348) reported that "the male did not appear to accomplish emission [of sperm] throughout the abortive procedure." The importance of the flagellum during sperm transfer is emphasized by the comparison between the weakly modified, relatively uniform flagellum of Eremobatidae, with direct sperm transfer, and the highly modified flagellum of taxa, e.g., Solpugidae, with indirect sperm transfer. Unfortunately, no relevant data are available for other taxa with a setiform flagellar complex and flagella that are reduced or absent (i.e., Lipophaginae and Melanoblossiinae).

Taxonomic Diversity of the Flagellar Complex

Ammotrechidae: The composite flagellum of Ammotrechidae (pls. 34E, F, 35F, G, 40J, K) is a fixed (nonrotatable) membranous, oval bowl-shaped structure (Muma, 1976) comprising a stalk and a base (table 16). The short stalk connects the base to the cheliceral finger prodorsally. The stalk attaches and is fixed to the sclerotized oval internal margin of the socket such that the apex of the flagellum is distally directed (pl. 146A, E, G, I).

The margins of the flagellum curve prolaterally (i.e., away from the prolateral surface of the chelicera) in Ammotrechidae, unlike Mummuciidae, in which they curve ipsilaterally (i.e., toward the prolateral surface of the chelicera). The margins are usually minutely fringed, often more so where the bowl-shaped structure opens distally (Iuri et al., 2014: 25, 22, figs. 2, 4), and fine hairs or spicules, important for species diagnosis (Iuri et al., 2014: 23), cover the surface in many species (e.g., Botero-Trujillo, 2014: 325, fig. 15).

According to Roewer (1934: 138, fig. 133b, c, reproduced here in fig. 22E), the flagellum comprises a narrow lumen between two membranous walls, which is restricted to the proximal part of the flagellum and disappears toward its apex. The lumen is presumably connected to the hemolymph in the chelicera via the attachment point, and hemolymph pressure in the flagellum is presumed to increase by contraction of muscles in the cheliceral manus during copulation (Roewer, 1934: 138). However, Maury (1984: 756, fig. 3) neither illustrated two membranous walls in a cross section of the ammotrechid flagellum, nor provided a description thereof.

No modified spiniform setae are associated with the flagellum of Ammotrechidae and, except for the flagellum itself, the proventral distal (*pvd*) setae are undifferentiated.

Ceromidae: Except for *Toreus*, in which the flagellum is apparently absent, the flagellum of Ceromidae (pls. 32A, B, 33A–C, 91A, C, G, I) is composite, and comprises a stalk, base and shaft (table 16). The ceromid flagellum was erroneously described as "immovably fixed" by Purcell (1899: 395). It can rotate paraxially through 180°, and the apex is directed proximally in the resting position. The shaft varies from sclerotized and whiplike, e.g., in *Ceroma*, to semisclerotized or membranous and partially whiplike, in *Ceromella*. As in Solpugidae, the sclerotized flagellum is minutely serrate along the shaft (pl. 41L), especially toward the apex. The base is swollen (capsular) with a protruding longitudinal membranous section prolaterally that appears to hold the alembic fluid, and may be homologous to the alembic pouch of Solpugidae. A similarity between the swollen base of the flagellum of Ceromidae and the bulbous base of the flagellum of Solpugidae was first noted by Pocock (1897), while Roewer (1934: 148) suggested that the small enlargement at the "base" of the flagellum (the basal peg) of *Karschia* is similar to the base of the flagellum of Ceromidae. The base of the flagellum of Ceromidae is attached to the cheliceral fixed finger via a short but distinct stalk situated in a highly sclerotized socket (pl. 96). A cross section of the flagellar shaft of *Ceroma inerme* prepared during the present study appears to show two lumens, an alembic lumen and a hemolymph lumen (pl. 41K–N). Roewer (1934: 140) reported that the shaft is blind ending apically. If an alembic lumen is present, however, it would be connected to the exterior via an apical pore, indications of which were found in *Ceroma inerme* (pl. 41M). The hemolymph canal narrows and eventually disappears toward the apex (pl. 41N). Hemolymph in the shaft does not connect to the exterior, and hemolymph pressure is thought to cause the flagellum to rotate (Roewer, 1934: 148).

The base of the flagellum of Ceromidae is obscured behind a fanlike array of three to eight rigid flagellar complex plumose (*fcp*) setae arising from a small elevation. The number of setae depends on the species and on which setae are included in the count. These setae, which appear to protect the base of the flagellum (Purcell, 1899; Hewitt, 1935), tend to be distinctly narrowed apically and are often shaped like a pipette, comprising a long, broad, markedly sclerotized cylindrical base, and a narrow, extended, and weakly sclerotized apical section, which may or may not be plumose (plumosity hypothesized to be secondarily reduced or lost). Two or three flagellar complex spiniform (*fcs*) setae (*Oberfingerdornen* sensu Roewer, 1934: 148), situated dorsolaterally on the fixed finger near the base of the flagellum, characterize some species. For example, two *fcs* setae are present in *Ceroma langi* Hewitt, 1935 and *Ceroma ornatum* (pl. 93B, C) whereas three are present in *Ceroma sylvestris* Lawrence, 1938 and *Ceromella focki* (Kraepelin, 1914).

Daesiidae: The composite flagellum of Daesiidae is used extensively in the systematics of the family, due to its many diverse shapes. The flagellum can rotate paraxially through 180°, its apex being directed proximally in the resting position, unlike the immovably fixed flagellum, with a distally directed apex, of Ammotrechidae and Mummuciidae. A shaft is absent, and the flagellum is typically membranous in Daesiidae, except in *Ammotrechelis* (pls. 32F, 33H), *Namibesia* (pls. 32E, 33G), and *Syndaesia* (table 16). The flagellum is connected to the flagellar socket via a stalk that is usually very short and indistinct. The stalk is attached gradually to the base, e.g., in *Ammotrechelis*, *Biton*, and *Gluvia*, in such a manner that the attachment represents a hairpin to kidney shape (e.g., pl. 40G–I). The flagellar stalk is situated at the proximal end of the membranous flagella of *Blossia* and *Hemiblossia* (pl. 34C, D) and more medially on the membranous flagella of other Daesiidae, e.g., *Biton* and *Gluvia* (pl. 34A, B). The point of attachment of the stalk to the flagellum may be phylogenetically informative.

The margins of the membranous flagellum of most daesiids may be shallowly curved inward, forming a bowl-shaped structure, or deeply curved inward, forming a husk- or vesicle-shaped structure, and variations thereof. The longitudinal aperture, where the two margins of the membranous flagellum converge, faces away from the prolateral surface of the chelicera in Daesiidae, unlike the membranous flagellum of Mummuciidae, in which the aperture faces toward the prolateral surface. The edges of the membranous flagellum of Daesiidae are usually fringed, especially toward the apex, and fine hairs or spicules, important for species diagnosis, cover its surface in many species. A midrib, which may terminate in a distal hooklet, extends medially along the length of the membranous flagellum in some species of *Blossia* (pl. 34C, 35C).

Roewer (1934) did not illustrate the membranous flagellum of Daesiidae in cross section but, based on its similarity to the membranous flagellum of Ammotrechidae (Roewer, 1934: 138, fig. 133b, c), it presumably also comprises a narrow lumen between two membranous walls. The lumen is probably also connected to the hemolymph, and the flagellum may function when hemolymph pressure increases by contraction of the muscles in the cheliceral manus during copulation. No sign of hemolymph was seen in the present study, however.

Two monotypic genera, *Namibesia* (Namibesiinae) (pl. 132A) and *Syndaesia* (vide Maury, 1985), are unique among Daesiidae in possessing a composite flagellum that is long, sclerotized, and whiplike, comprising a stalk, base and shaft, and more closely resembles the whiplike flagella of Ceromidae, Hexisopodidae, and Solpugidae than those of other daesiids. A hemolymph lumen and an alembic lumen appear to be present in the shaft of *Namibesia*. The stalk, base, and manner of attachment of the flagellum of *Namibesia*, and probably also of *Syndaesia*, are particularly similar to the flagellum of Hexisopodidae (pl. 32C, E).

The flagellum of *Ammotrechelis goetschi* also comprises a stalk, base, and shaft, and appears to be intermediate in form between the whiplike and membranous flagella, possessing both bowl-shaped and whiplike sections (pl. 32F). The bowl-shaped section, or base, of the flagellum of *A. goetschi* is considered homologous to the membranous flagellum of most Daesiidae, Ammotrechidae, and Mummuciidae, as well as to the base of the whiplike flagellum of Ceromidae, Hexisopodidae, Solpugidae, and the daesiids, *Namibesia* and *Syndaesia*, supporting the hypothesis that the base of the whiplike flagellum is homologous to the various types of membranous flagella. The broad shaft of the flagellum of *A. goetschi* is considered homologous to the shaft of Ceromidae, Hexisopodidae, Solpugidae, and the daesiids, *Namibesia* and *Syndaesia*. Two canals, probably representing a hemolymph lumen and an alembic lumen, are visible in the shaft.

Spiniform setae associated with the flagellar complex (*fcs*) are absent in Daesiidae. The modified spiniform setae of *Gnosippus klunzingeri* males are unlikely to be part of the flagellar complex, but may be associated with its apparently fossorial habitus. Setiform setae, on the other hand, are more differentiated in males of some species of *Blossia*, e.g., *B. falcifera dolichognathus* Hewitt, 1921, currently in synonymy with *B. falcifera* Kraepelin, 1908, *B. filicornis*, and *B. grandicornis* (e.g., pl. 139C; Hewitt, 1921: 10, fig. 4). In these species, the three distalmost proventral distal (*pvd*) setae are slightly more robust, and arranged into a cluster, slightly separated from the rest of the *pvd* series. Hewitt (1921) noted a similarity between these setae and the setae situated at the base of the flagellum of Ceromidae, and suggested that they may protect the flagellum in the resting position.

Dinorhaxinae: The filiform flagellum of *Dinorhax* is sessile and immovably fixed to the fixed (dorsal) finger. It is unique among the flagella of solifuges in its orientation to the finger, projecting ventrally although it is distally directed at the point of attachment. The flagellum of *Dinorhax* is a thin, straight, and semisclerotized structure with a markedly setal appearance (pls. 30E, 31C). It is inserted parallel to the finger in a small, swollen protrusion. The entire surface of the flagellum is covered in minute spicules. A pronounced sulcus is present along its length. No alembic lumen is visible in cross section, but the sulcus appears to protrude into the lumen. The cuticle surrounding the lumen is lined by fine ridges and microstructures that appear to be spiculate (pl. 41A). The filiform shape of the flagellum and the sulcus along its length resemble the filiform shape and plumose row of setae along the length of the flagellum of the karschiid, *Karschia*. The flagellum of *Dinorhax* probably evolved in a similar manner to that of *Karschia*, and both probably function similarly, by means of hemolymph pressure.

Two or three setae, situated dorsal and ventral to the point of attachment of the flagellum of *Dinorhax*, are slightly more differentiated from the remaining setae near the apex of the finger, and probably homologous to the *pdd* and *pvd* setae, respectively.

Eremobatidae: Eremobatidae possess a **type A setiform flagellar complex (*type A sfc*)** which is usually a heterogeneous assemblage of modified setae, most often belonging to the prodorsal distal (*pdd*) and proventral distal (*pvd*) series, often including a setiform flagellum (pls. 37–39; table 17). Modified setae in the *sfc* may also include promedial (*pm*) setae, e.g., in *Eremocosta titania* (pls. 39I, 72A) or, rarely, proventral subdistal (*pvsd*) setae, e.g., in *Eremothera sculpturata* Muma, 1951 (pls. 39J, 72E). The *type A sfc* differs from the *type B* and *type C sfc* in that it does not appear to ever consist entirely of *pvd* setae. The *type A sfc* is further categorized by the convergence of *sfc* setae toward or along the fixed finger.

The various forms of *sfc* in eremobatids were well documented by Muma (1951, 1970a, 1989) and are summarized in table 15. The *sfc* of *Eremobates* and, often to a lesser extent, *Eremochelis* comprise a modified apical seta, hypothesized to be the primary flagellum, which demarcates the boundary between the **setiform flagellar complex (*sfc*) dorsal series** and **setiform flagellar complex (*sfc*) ventral series** (pls. 38A, B, 39A–F). Both series are situated in a narrow recess of the asetose area of the fixed finger and hypothesized to be homologous to the prodorsal distal (*pdd*) and proventral distal (*pvd*) series of setae,

TABLE 17

Types of setiform flagellar complex in Solifugae

Abbreviations: **FF,** fixed finger; **MVE**, medioventral excrescence; ***pdd*,** prodorsal distal setae; ***pm*,** promedial setae; ***pvd*,** proventral distal setae (plumose); ***pvsd*,** proventral subdistal setae; ***sfc*,** setiform flagellar complex.

	Type A	*Type B*	*Type C*
Taxon	Eremobatidae Kraepelin, 1901	Lipophaginae Wharton, 1981	Melanoblossiinae Roewer, 1933
Setal origin	*pdd*, *pvd*[a]	*pvd*	*pvd*
Flagellum	present or absent	absent	present or absent
Cluster	ill defined	well defined	well defined and demarcated (distinct unit)
Concavity	absent or present, as flagellar groove or ventrodistal concavity	absent	present, as *sfc* depression
Relation to FF	converging toward, arranged along, narrow FF	none	promedial on broad FF; protected by MVE
Additional setae			*sfc principal seta*

[a] rarely *pvsd*, *pm*.

respectively. The setiform flagellum originates distalmost, consistent with its origin from the ventral flagellar seta (*vfs*) (pl. 46A). The flagellum varies from a flat, membranous, bladelike structure, fringed at the margins, e.g., in *Eremobates* (pls. 38, 39A–E; Muma, 1951: 53, fig. 46), to a short, barely visible plumose seta, e.g., in *Eremochelis insignatus* (pl. 76E). The flagellum is never prominent, but rather is concealed by other modified and unmodified setae that form a cluster. In *Eremobates* and some species of *Eremochelis*, the flagellum is situated within a groove extending along the prolateral surface of the fixed finger (pls. 38, 39A–E). In other taxa, the prolateral groove is absent, or differs in position, shape, and length, characters used extensively in eremobatid systematics (Muma, 1951: 39).

In *Eremocosta*, the *sfc* is weakly differentiated, with minor modifications to setae of the *pdd*, *pvd*, and apparently the *pm* series, involving slight increases in length and thickness, and a flagellum, as defined in the present contribution, is absent (pls. 37C, 39I). A flagellar groove is absent, but a deep, ovate, retroventral or ventral concavity, referred to here as the **ventrodistal concavity**, is present (pls. 37C, 73B).

Species of *Eremothera*, e.g., *E. sculpturata* (pls. 37B, 39J, 74A), are unique in possessing markedly prolaterally directed setae in the ventral series, which not only comprises proventral distal (*pvd*) setae, but also includes the comb of the proventral subdistal (*pvsd*) series. A flagellum appears to be absent, but the *sfc* dorsal series, comprising modified *pdd* setae, consists of stiff, tubular setae as well as two broad, flat setae situated apically in the *pdd* series.

The *sfc* of several other eremobatid genera mainly comprise modified *pdd* setae, without a flagellum. Species of *Eremorhax*, e.g., *E. joshui*, possess a homogeneous cluster of setae in the *sfc* that appears to consist only of *pdd* setae, although the affinity of the different setae in the *sfc* is unclear, and it may also include *pvd* setae modified similarly to the *pdd* setae. The *sfc* of *Chanbria* comprises elongated, weakly striated *pdd* setae and similarly elongated *pvd* setae, without a flagellum in all described species. The *sfc* of *Hemerotrecha* is characterized by slightly to markedly modified *pdd* setae in the dorsal series. These setae may be homogeneous, forming a row of three or four similarly modified setae, as in *H. hanfordana* (pl. 37D) or heterogeneous, with two clavate distal setae followed by a row of less modified *pdd* setae, as in *H. branchi*. Although situated distally in the *pdd* row, none of these more distinct setae are situated apically, implying that none is a modified *vfs* and a flagellum is therefore absent. A small, ventrodistal concavity, the mesal ventral groove sensu Brookhart and Cushing (2008: 50, fig. 3), is present in some *Hemerotrecha*.

Setae within the *sfc* differ in shape (round or flat, curved or straight, etc.), plumosity/striation, and robustness. Setae of the ventral series, derived from the *pvd* series, are slightly to moderately modified and usually homogeneous within species whereas setae of the dorsal series, derived from the *pdd* series, are often more markedly, and not necessarily uniformly, modified.

References to apical plumose bristles (e.g., Muma, 1951: 51, 99), setae (e.g., Muma, 1951: 110), or spines (e.g., Muma, 1951: 82), indicating distal setae differentiated from other setae in the *sfc*, typically refer, albeit unintentionally, to the flagellum. A second modified seta, situated ventral to the flagellum and usually very indistinct, referred to as the subapical plumose seta (subapical plumose bristle in the literature, e.g., Muma, 1951: 51, 99), may be present, e.g., in *Eremobates chihuaensis* Brookhart and Cushing, 2002 (pl. 39E).

New World workers place more emphasis on the shape of the flagellar groove than on the flagellum, which is seldom depicted in figures, except in a few cases, e.g., Muma (1951: 53, fig. 46) and Brookhart and Muma (1981: 291, figs. 2, 3). Muma (1970a) used broad differences in apical setal morphology to distinguish between *Eremobates* and *Eremorhax*, however, and a detailed survey with modern imaging techniques may reveal the flagellum to be of greater significance in eremobatid systematics than currently appreciated.

Galeodidae: The sclerotized, spoon-shaped flagellum of Galeodidae is considered to be sessile. It has been described as “extremely” mobile, and is subdiaxially rotatable, able to turn 180° (Sørensen, 1914: 34; Roewer, 1934: 145; Muma, 1976: 4). The apex is directed proximally in the resting position. Unlike the rotatable flagellum of other taxa, i.e., Ceromidae, Daesiidae, and Hexisopodidae, the flagella of galeodid specimens preserved in 90% ethanol were either immovable, or reverted to their original positions when released, consistent with descriptions that the flagellum of Galeodidae is nonrotatable (e.g., Klann, 2009). This suggests a difference between the attachments of the sessile flagellum of Galeodidae and the rotatable composite flagella of Ceromidae, Daesiidae, and Hexisopodidae, which retain the ability to rotate, as well as their distinct resting position, after fixation.

The galeodid flagellum has been variously described as ramiform, spoon shaped (*cuilleriforme*), capitate, and leaflike (pls. 30G, 31E; Sørensen, 1914: 34; Birula, 1929a: 163; Roewer, 1934: 149; Muma, 1976). The stem or **peduncle** flattens distally into a blade or **scapus** (Birula, 1916, 1925), the concave inner surface of which is finely plumose. Interspecific variation in the flagellum of Galeodidae is subtle and includes such characters as the peduncle to scapus ratio, the shape of the base of the scapus (asymmetric versus symmetric), and/or the manner in which the flagellum tapers apically (e.g., Birula, 1936a, 1938: 111, fig. 74). The terms stalk and stem, although often used as synonyms of peduncle, are not assumed to be homologous to the stalk as defined here (table 16), and peduncle is preferred.

The flagellar socket of Galeodidae is situated in a deep depression (alveolus) that resembles the alveolus of *Karschia* and Rhagodidae. The proximoventral margin of the alveolus is slightly elevated to form the socket margin elevation (sme), which is most similar to the sme of *Karschia*, but also resembles that of *Eusimonia* and Rhagodidae.

The flagellum of Galeodidae appears to have altered little from its original setal form. Roewer (1934: 150, fig. 147) provided cross sections, which indicate a hollow peduncle and a small, retrolaterally compressed lumen in the scapus (blade). Hemolymph pressure inside the lumen of the flagellum was suggested to cause it to rotate forward (Sørensen, 1914: 167; Roewer, 1934: 149). A hollowed peduncle was confirmed in the present study, but the presence of a lumen in the scapus was equivocal (pl. 41B–D).

One to four flagellar complex spiniform (*fcs*) setae, usually blunt and apically flattened, are situated proximoventral to the point of attachment of the flagellum of Galeodidae (Birula, 1929a: 164, fig. 1; 1929b: 276, fig. 2; 1937a: 595, fig. 17; 1938: 155, fig. 87). These setae appear to be modified prodorsal distal (*pdd*) setae, based on their insertion adjacent to the prodorsal distal margin (pddm) of the fixed finger (pl. 4C). The *fcs* setae of galeodids usually decrease in size proximally (Birula, 1936a, 1937a: 594). Variation in the number of *fcs* setae (e.g., one on the sinistral and three on the dextral chelicera, or two on the sinistral and four on the dextral) has been reported on the same individual (Lawrence, 1954) or among conspecifics (e.g., Lawrence, 1956: 132; Birula, 1937b: 584), and the *fcs* setae are therefore uninformative for species delimitation.

A well-differentiated, stout flagellar complex plumose (*fcp*) seta and occasionally a second, weaker plumose seta are situated directly proximoventral to the flagellum of Galeodidae (pls. 4C, 63A, D). The *fcp* seta, first noted by Birula (1937a, 1937b; 1938), probably belongs to the *pvd* series and assumed a more dorsal position due to a shift in the position of the flagellum and the remaining *pvd* setae.

Gylippinae: The flagellar complex of Gylippinae was discussed by Birula (1913). The membranous, straplike flagellum of Gylippinae is uniquely situated entirely on the sclerotized area of the fixed finger, to which it is partially fused (pls. 4D, 32H, 33I, J). Similarities with the basal part of the flagellar shaft of Solpugidae suggest it is homologous with the whiplike flagella and it is therefore regarded as a composite flagellum (table 16). If the flagellum of Gylippinae is indeed composite, the absence of a base would be unique (the stalk is indistinct in Solpugidae, but the bulbous base is prominent), and must be regarded as a secondary loss. Alternatively, the absence of a base (and stalk) may imply that the flagellum of Gylippinae is sessile. The shaft of the flagellum of Gylippinae is anteriorly to anterodorsally directed at its apex. The section that remains attached is straplike, but the apex varies (Gromov, 1998: 181, fig. 1s; Birula, 1938: fig. 62c), e.g., it is jagged in *Gylippus* (*Anoplogylippus*) *pectinifer* Birula, 1906, and pointed in *G.* (*Hemigylippus*) *krivokhatskyi* Gromov, 1998. The apex is reportedly bifid (Birula, 1938: fig. 58e) in *G.* (*A.*) *rickmersi* Kraepelin, 1899, currently in synonymy with *G.* (*A.*) *ferganensis* Birula, 1893. Roewer (1934: 141) interpreted the bifid apex as "two papillae," each representing a separate flagellum homologous to the two rhagodid flagella. However, the putative "papillae" originate from the same structure, consistent with a single flagellum.

The lumen of the flagellum appears to be connected to the hemolymph in the cheliceral manus, the hydraulic pressure of which is assumed to straighten the flagellum during mating (Roewer, 1934: 142).

One or two prominent, robust flagellar spiniform (*fcs*) setae are situated prodorsally near the base of the fixed (dorsal) finger of adult male *Gylippus* (*Gylippus*) and *Gylippus* (*Paragylippus*) (pls. 85A, B, 86A, B). The *fcs* seta/e, the *Oberfingerdorn* of Birula (1913: 322) and *Spina digitalis* of Roewer (1934: 308), is hypothesized to be a modified prodorsodistal (*pdd*) seta/e. Another large, robust spiniform seta is situated on the retrolateral surface of the cheliceral manus of male Gylippinae. This seta, the *Mandibulardorn* of Birula (1913: 322), the *Spina principalis* of Roewer (1934: 308), and the mandibular spine of Gromov (1998: 184), is referred to here as the retrolateral manus spiniform (*rlms*) seta (pls. 85B, 86A, B). The flagellar complex spiniform (*fcs*) seta/e and the retrolateral manus spiniform (*rlms*) seta of Gylippinae are the largest, most robust setae on the chelicerae of solifuges. The location of such a highly modified seta on the retrolateral surface of the chelicera is also unique because distinct modifications of one or two setae are usually restricted to the prolateral or prodorsal surfaces of the chelicera in solifuges, the only exceptions being some modified retrolateral finger setae (the *principal rlf* setae) in other families, especially Daesiidae. A possible homolog of the *rlms* seta of male Gylippinae may also be identified in females (pl. 85D, F, arrows; Birula, 1913: pl. VIII, fig. 1).

The *rlms* and *fcs* setae are used extensively in the systematics of Gylippinae (Birula, 1913) and appear to be stable in number, position, and shape. Indications of variation in the literature may be misleading. For example, a single *rlms* seta was reported in *Gylippus* (*P.*) *monoceros* by Birula (1913) and Roewer (1933: 314, fig. 229B), as in the specimen examined in the present study (pl. 85B), whereas two *rlms* setae were depicted by Koç (2011: 120, fig. 3). However, other differences between the specimens illustrated by Koç (2011: 120, fig. 3) and in plate 85B suggest they are not conspecific, implying that the different numbers of *rlms* setae may not be indicative of intraspecific variation. Different interpretations of the spiniform setae may also account for the apparent variation. For example, Roewer (1934: 308) distinguished *Gylippus* from other Asian gylippid genera by the presence of two *rlms* setae and one *fcs* seta, whereas Birula (1913: 322) diagnosed it on the basis of one *rlms* seta and "one or two" *fcs* setae. Based on Roewer's (1934: 311) figure 228$A_{1,2,}$ B_1, the second *rlms* seta reported by Roewer (1934) and the second *fcs* seta reported by Birula (1913) appear to be the same seta, interpreted differently by the two authors, thus accounting for the different numbers provided in the generic diagnoses.

HEXISOPODIDAE: The composite hexisopodid flagellum (table 16) comprises a stalk, cuplike base, and whiplike shaft that is usually laterally compressed (pls. 32C, D, 33D–F, 129). Although reported as immovable by Muma (1976, 1982), the flagellum of Hexisopodidae is paraxially rotatable, with the apex directed proximally in the resting position. The whiplike, strongly curved shaft originates from a cuplike base, attached near the base of the fixed (dorsal) finger via a short but distinct stalk (pl. 32D). The flagellum is largely hidden between the two chelicerae. Interspecific differences concern the apex and degree of expansion of the laterally compressed shaft (pl. 33D, E). The shape of the cuplike base may vary intraspecifically, e.g., in *Hexisopus lanatus* (vide Purcell, 1902) and *Hexisopus pusillus* (vide Wharton, 1981). The swollen base of the flagellum of Hexisopodidae resembles the capsular base of the flagellum of Ceromidae, but differs in being open, forming a cuplike structure, rather than a capsular base. The cuplike flagellar base of Hexisopodidae (pl. 40F) is very similar to that of the daesiid genus, *Namibesia* (pl. 40E). Roewer (1934: 148) did not provide a cross section of the flagellum of Hexisopodidae, but noted its similarity to the flagellum of Ceromidae. According to Roewer (1934: 140), the flagellum of Hexisopodidae is blind ending apically, but indications of an external opening are evident (pl. 41G) in accordance with the presence of an alembic lumen, as reported by Lamoral (1975) and confirmed in the present study (pl. 41F–J). The hemolymph lumen partly surrounds the alembic lumen, and the hexisopodid flagellum probably rotates by hemolymph pressure. The similarity of the flagella of Ceromidae, Hexisopodidae, Solpugidae, and *Namibesia* suggests a common origin.

A small field of short, stout spiniform setae, the **prodorsal spiniform setal cluster**, or ***pdsc***, is present on the prodorsal surface of the chelicera, directly ventral to the callus and proximal to the sclerotized area of the fixed finger, in some male *Chelypus* (pls. 32C, 33E, 130D; Hewitt, 1919b; Lamoral, 1973), and forms part of the flagellar complex of hexisopodids.

KARSCHIIDAE: Two very different flagella and flagellar complexes occur in Karschiidae. *Karschia* has a coiled, filiform flagellum (pls. 30A, 31A, 50–52) considered to be sessile (table 16). It retains a basic resemblance to a plumose seta, often with a fine fringe of hairs, mistakenly termed "cilia" by Lawrence (1954: 112), along one side (Roewer, 1934: 142) or other microstructures on the shaft, labeled *uc* in Birula (1938). It is rotatably attached to the fixed finger via a short stalk situated in a deep alveolus similar to the alveolus of Galeodidae and Rhagodidae, the proximoventral margin of which is slightly elevated to form the socket margin elevation (sme), which is most similar to the sme of Galeodidae, but also resembles that of *Eusimonia* and Rhagodidae. The "base" of the flagellum of *Karschia* comprises a slight swelling from which a small excrescence, the **basal peg** (*Zapfen* of Roewer, 1934: 148) emerges (pls. 30A–C, 40C; Birula, 1938: fig. 20). The basal peg appears to halt the flagellum during its putatively rapid, forward extension caused by hemolymph pressure (Roewer, 1934: 146). Roewer (1934: 148) suggested a similarity between the basal peg of *Karschia* and the base of the flagellum of Ceromidae. The flagellum of *Karschia* therefore resembles the composite flagellum in the presence of a distinct stalk, a basal peg with similarities to the base of the whiplike flagellum, and an elongated filiform structure that could be interpreted as a shaft. Roewer (1934: 145, fig. 143 A_1, reproduced here as fig. 22A) described and illustrated the flagellum of *Karschia* as an elongate double-walled tubelike structure, which formed from a seta that broadened along its length, the margins rolling inward until almost forming a closed canal. Roewer's (1934) hypothesis that the flagellum of *Karschia* formed by longitudinal infurling is consistent with the longitudinal plumose fringe on the flagellum, but the hypothesized double membrane may have been lost. Hemolymph appears to be present in the lumen of the flagellum, whereas an alembic canal appears to be absent. Therefore, although the flagellum of *Karschia* resembles a composite flagellum, in which the equivalent of a "stalk," "base," and "shaft" can be identified, it is considered sessile pending further investigation.

The flagellar complex of *Karschia* (pls. 30A, 31A, 50–52) comprises various structures comprehensively labelled by Birula (1938: 46: fig. 20): a long, usually coiled, filiform flagellum; plumose setae, situated directly ventral to the flagellum and modified to various degrees, including broadening (*Säbelborsten* of Kraepelin, 1908a: 222; Birula, 1938; Gromov, 1998: 181, figs. 1f–i), referred to here as the flagellar complex plumose (*fcp*) setae; and one or two acuminate subspiniform setae, typically swollen basally and situated dorsoproximal to the point of flagellar attachment, labeled, distal to proximal, *k* and *c* by Birula (1938), and referred to here as the flagellar complex subspiniform (*fcs*) setae. Based on their position relative to the flagellum in species such as *Karschia* (*K.*) *tibetana* Hirst, 1907, Hirst (1907) and Kraepelin (1908a: 221, fig. 57) suggested that the *fcs* setae function to stabilize the coiled structure of the flagellum.

Barrussus and *Eusimonia* each bear two distinct, interspecifically variable, membranous or weakly sclerotized flagella that are both considered to be sessile (pls. 30D, 31B, 53–55): a broad, thin, dorsal secondary flagellum and a tubelike ventral primary flagellum. The literature is inconsistent, however, concerning which structure is interpreted as the flagellum (table 14). The ventral (primary) flagellum often closely resembles that of rhagodids. Panouse (1955: 347) also suggested a resemblance between the primary flagellum of *Eusimonia cornigera* Panouse, 1955, and the flagellum of galeodids. The primary and secondary flagella of *Barrussus* and *Eusimonia* arise close to one another on the finger, but remain distinct. Both flagella appear to be immovably fixed to the finger. According to Panouse (1955), however, they are able to move through 90° from vertical to horizontal. This could not be verified in the present study. The proximodorsal margin of the socket of the primary flagellum is elevated to form a socket margin elevation (sme) most similar in form to the sme of the alveolus of Rhagodidae, but also resembling the sme of the alveolus of *Karschia* and Galeodidae. Both flagella are blind ending apically, and indications of a viscous milky substance suggest that the lumen of each is connected to the hemolymph (pl. 30D). *Barrus* appears to possess a secondary flagellum, but the literature is contradictory concerning whether a primary flagellum is present (Kraepelin, 1901: 140) or absent (Roewer, 1934: 306, fig. 227A).

One or two modified subspiniform setae situated dorsally on the fixed finger of some species of *Eusimonia* are hypothesized to be modified prodorsodistal (*pdd*) setae, and referred to here as flagellar complex subspiniform (*fcs*) setae (pls. 30D, 31B). A long, distally directed spiniform seta inserted prolaterally on the fixed (dorsal) finger, identified by Panouse (1955) as a third structure in the flagellar complex of *Eusimonia cornigera*, in addition to the primary and secondary flagella, is probably also a *fcs*. Additional setae may be modified in some species (Roewer, 1934: 143, fig. 141C), e.g., *Eusimonia mirabilis* Roewer, 1932.

Lipophaginae: Southern African lipophagines possess a weakly to strongly differentiated **type B setiform flagellar complex (*type B sfc*)** without a flagellum, i.e., no single seta in the complex is clearly differentiated from the others (pl. 36A–F). Unlike the *type A sfc* of Eremobatidae, the flagellar complex of Lipophaginae appears to consist entirely of modified proventral distal (*pvd*) setae, which have shifted dorsally and are usually uniformly modified, i.e., all setae in the complex are similar, or nearly so, in shape, length, etc. Unlike the *type C sfc* of Melanoblossiinae, which also consists entirely of modified *pvd* setae, the setae in the *type B sfc* are not arranged into a well-defined unit (pl. 36). Three or four plumose setae, which appear to have shifted dorsally, are more robust and distinctly more plumose than the other *pvd* setae in *Lipophaga trispinosa* (pls. 36B, 89A). In *Bdellophaga angulata*, the *pvd* setae also appear to have shifted dorsally, and the *sfc* consists of the apicalmost eight *pvd* setae, which form a brushlike cluster, intertwined apically into a "fused concave cushion" (pl. 36C, D; Wharton, 1981: 41), directly ventral to which approximately four *pvd* setae are modified and apically angular (pl. 36C, E, F). The *pvd* setae are unmodified in *Trichotoma michaelseni* (pl. 36A). Although some *pdd* setae are slightly more robust in males of *T. michaelseni* than in females (pl. 87A–F), they do not form a distinctly differentiated setal cluster, and a *type B sfc* is interpreted as absent.

Melanoblossiinae: Melanoblossiinae possess a **type C setiform flagellar complex (*type C sfc*)**, comprising several modified proventral distal (*pvd*) setae, including a setiform flagellum and/or a **setiform flagellar complex principal seta (*sfc principal seta*)**, arranged in a compact cluster to form a well-defined unit (fig. 26, pl. 36G–I; Purcell, 1903a; Wharton, 1981). The setae of the *type C sfc* appear to comprise two rows, a distal row of setae with limited plumosity (probably homologous to the ventralmost row in the *pvd* series of subadult males) inserted below a row of markedly plumose, highly modified setae (probably homologous to a more dorsally situated row of *pvd* setae in subadult males). These rows originate from a shallow elevation into a broad, shallow depression, the **flagellar complex depression** on the prolateral surface of the fixed (dorsal) finger (fig. 26C, pl. 36G–I), which is protected by a convex ventral enlargement of the finger, the **medioventral excrescence (MVE)**. Generic level differences are obvious in the *sfc* of *Lawrencega* and probably *Unguiblossia*, compared to *Melanoblossia*. The *sfc principal seta* is long in *Melanoblossia* and short in *Lawrencega*. The distal row of the *sfc* originates from the same shallow elevation as the proximal, plumose row in *Melanoblossia*, whereas only the proximal row originates from the shallow elevation, the distal row being inserted far distal to it, in *Lawrencega* (Wharton, 1981: 53, in key). The *sfc* setae tend to be more distally directed and more linearly arranged in *Melanoblossia* than in *Lawrencega*, in which their arrangement is more curved (Wharton, 1981: 53, in key).

The *type C sfc* of Melanoblossiinae is similar to the *type B sfc* of Lipophaginae in that all setae in the *sfc* appear to be derived from the *pvd* series, unlike the *type A sfc* of Eremobatidae, which may be derived from the *pdd*, *pvd,* and, rarely, the *pvsd* and *pm* series. The *type C sfc* differs from both the *type A* and *type B sfc* in that the setae are arranged into a well-defined unit situated medially on the prolateral surface of the fixed finger (table 17).

As in Eremobatidae, the setae of the flagellar complex (*sfc*) of Melanoblossiinae are often collectively referred to as a flagellum consisting of modified setae (e.g., Muma, 1976: 3; Wharton, 1981: 53; El-Hennaway, 1990: 24; Harvey, 2003:

199). However, only one of these setae is homologous to the flagellum, as defined in the present contribution. Purcell (1903a: 6) was the first to identify a single seta as the flagellum of *Melanoblossia*, i.e., the dorsalmost seta in the flagellar complex: "flagellum not rotatable, consisting of a flexible, densely hairy rod directed forward and lying against the inner surface of the jaw, and so completely hidden between the chelicerae." Identification of the flagellum of Melanoblossiinae remained challenging, however (see section on Homology of the Flagellum). According to Purcell (1903a: 7, 8, figs. 4, 6), the seta regarded as the flagellum (pl. 42, arrow) is distinct in *Melanoblossia globiceps* Purcell, 1903 but less so in *M. braunsi*, while Lawrence (1929: 176) noted that the flagellum is "not apparent" in *Lawrencega hewitti* (Lawrence, 1929), the type species of the genus.

Based on positional criteria, the seta homologous to the primary flagellum of the order is the dorsalmost seta in the distal row of setae, situated partly or entirely below the markedly plumose row of setae in the *sfc* ("a" in pl. 36G–I), not the seta traditionally regarded as the flagellum (Purcell, 1903a; Kraepelin, 1908a). The seta regarded as the flagellum of Melanoblossinae is slightly differentiated (longer) from other *sfc* setae, including those ventral to it in the same row, e.g., in *Lawrencega procera*. Whereas the flagellum is the most differentiated seta in the *sfc* of *Lawrencega* ("a" in pl. 36G, I), the *sfc principal seta* ("b" in pl. 36G–I) is the most differentiated seta in the *sfc* of *Melanoblossia*, in which it was historically regarded as the flagellum (Purcell, 1903a; Kraepelin, 1908a), and is relatively less differentiated in *Lawrencega*. Both the flagellum and the *sfc principal seta* are distinctly differentiated in the *sfc* of an undescribed species of *Melanoblossia* (fig. 26). A survey of the *sfc* of Melanoblossinae, using SEM, is needed to evaluate the presence and nature of the various modified setae, including the flagellum, in the *sfc*. Based on the prominence of the *sfc principal seta* in the *sfc* of *Melanoblossia*, this seta may be functionally more involved in mating behavior than the flagellum itself.

Although Muma (1976: 3), followed by Gromov (2003b: 199), suggested that the setae in the flagellar complex of Melanoblossiinae are "slightly movable," these setae do not appear to possess a greater ability to move than other unmodified setae. Each seta in the flagellar complex of Melanoblossiinae retains a fundamentally setal character, with the socket visible, albeit modified. The only study that alludes to the internal morphology of the flagellum of Melanoblossiinae, by Lamoral (1975), reported the presence of an alembic canal. This seems unlikely, however, because the alembic canal is a distinct, separate canal within the flagellum, with an external opening, which would be difficult to accommodate in a setiform flagellum of the type observed in Melanoblossiinae. The presence/absence of an alembic canal in the setiform flagellum needs further investigation.

MUMMUCIIDAE: The composite flagellum of Mummuciidae (pls. 34G, H, 35H, I) is a membranous, roughly ovoid, vesicular structure, comprising a stalk and a base, without a shaft, and is generally similar to the flagella of Ammotrechidae and most Daesiidae with membranous flagella (i.e., excluding Namibesiinae, *Syndaesia*, and *Ammotrechelis*) (table 16). It is attached prodorsally to the fixed (dorsal) finger through a very short stalk into an oval or circular flagellar socket inner margin (pl. 40L). Like Ammotrechidae and unlike Daesiidae, the flagellum of Mummuciidae is fixed (nonrotatable) and its apex is distally directed (pl. 34G, H).

The flagellum of Mummuciidae is vesicle shaped and often retrolaterally compressed, whereas the flagellum of Ammotrechidae is a more open, bowl-shaped structure. The margins of the flagellum curve ipsilaterally (i.e., toward the prolateral surface of the chelicera) in Mummuciidae, whereas the margins curve prolaterally (i.e., away from the prolateral surface of the chelicera) in Ammotrechidae and Daesiidae with a membranous flagellum. The vesicle of Mummuciidae thus possesses a small opening ipsilaterally, which may extend to form a distal opening (Maury, 1984; El-Hennawy, 1990;

González Reyes and Corronca, 2013). Xavier and Rocha (2001) were the first to describe a broad opening ipsilaterally along the length of the flagellum of Mummuciidae, and this was subsequently reported by others (Rocha and Cancello, 2002: 105, fig. 6; Martins et al., 2004; Carvalho et al., 2010). The flagellum is usually covered with spicules and fringed apically.

As with Ammotrechidae and most Daesiidae, the flagellum of Mummuciidae was hypothesized to possess double-walled sides enclosing a narrow lumen (Roewer, 1934: 138). Rocha and Cancello (2002) noted a “white viscous substance,” presumed to be hemolymph, filling the lumen. Therefore, as with the membranous flagella of Ammotrechidae and most Daesiidae, the narrow lumen of the flagellum of Mummuciidae is probably connected to the hemolymph in the chelicera.

A broad flagellar groove, situated longitudinally along the fixed finger, accommodates most of the flagellum in Mummuciidae. This groove, evident in material examined during the present study (pls. 34G, H, 35H, I) and in SEM images by Carvalho et al. (2010: 25, figs. 13, 15, 16), González Reyes and Corronca (2013: 542, fig. 5), and Botero-Trujillo (2014: 324, figs. 12, 13), is created by the compressed dorsal margin of the finger, the dorsal crest, which is slightly curved prolaterally to form a narrow carina dorsally, and by a similar, but less prominent carina ventrally.

Rhagodidae: As in the karschiid genera, *Barrussus* and *Eusimonia*, two flagellar structures, one ventral, the other dorsal, herein referred to respectively as the primary and secondary flagella, are present in Rhagodidae (pls. 30F, 31D). Both flagella, considered sessile (table 16), are immovably fixed to the fixed (dorsal) finger, with the apices dorsodistally directed. Sørensen’s (1914: 165) statement that the flagella are *très mobile* refers to their flexibility rather than their ability to move. The two flagella are situated close to one other in a distinct depression (the alveolus) in the fixed (dorsal) finger. A socket margin elevation (sme) on the dorsoproximal margin of the alveolus (pl. 40B) is most similar to that of *Eusimonia*, but also resembles the sme of *Karschia* and Galeodidae. The flagella are weakly plumose distally and each bears a membranous lamella, extending along its length. The manner in which each lamella is situated relative to the lamella of the adjacent flagellum creates a **diploflagellum** that superficially resembles a single concave, tubelike structure, the compound nature of which becomes evident only when the two flagella are pried apart. Each flagellum is, itself, tubelike with a longitudinal inner lumen extending along the entire length, and presumably connected to the hemolymph of the chelicera (Roewer, 1934: 140, fig. 137, reproduced here as fig. 22B, C). Hemolymph pressure in the lumen was suggested to cause the tube composed of the two flagella to open slightly (Sørensen, 1914: 167; Roewer, 1934: 141).

No additional structures or modified setae are present in male rhagodids, and the flagellar complex consists solely of the two flagella.

Solpugidae: The composite flagellum of Solpugidae consists of an indistinct stalk fused to the chelicera, a bulbous base, and a usually whiplike shaft (pl. 32G, 33K–M; table 16). The flagellum is immovably attached prodorsally to the fixed (dorsal) finger with the apex proximally directed. Although very diverse in form (Hewitt, 1919b), the flagella of all Solpugidae are characterized by a distinctly bulbous base with a more sclerotized shaft emerging distally from it (pls. 32G, 33K–M). A dorsal cuticular elevation of the fixed (dorsal) finger, here referred to as a **retrolateral convexity**, covers part of the bulbous base retrolaterally (fig. 25A, visible through the transparent bulbous base of the flagellum).

The bulbous base varies interspecifically in position, size, shape (e.g., from round to elliptical in prolateral view), extent of sclerotization, and disposition of the dorsal carina (fig. 25, pl. 45). The sides of the base are semitransparent and flexible (Roewer, 1934: 153), flat to concave prolaterally and slightly convex retrolaterally (pl. 48I).

The fixed finger possesses a flagellar groove dorsally or prodorsally, to which the base of the shaft is attached and along which it extends distally from the flagellar base for a short distance, before curving dorsally and then slightly or markedly proximally (pls. 45, 48). The length of the recurved shaft varies from very short, not surpassing the proximal margin of the bulbous base (pl. 49A, B), to very long, surpassing the ocular tubercle (pl. 110E, F). The shaft is usually a sclerotized cylindrical (rodlike or whiplike) or flattened (strap- or ribbonlike) structure, with various modifications (pl. 49A–C). The flagellum of *Solpuguna* Roewer, 1934 is unique because it does not curve dorsally, but follows the fixed finger for a distance before terminating apically in three or four fingerlike projections resembling a claw (pls. 48G–I, 49C), the alembic canal opening externally at the tip of one of the projections (pl. 48I, arrow). Minute denticles and microstructures, usually situated distally rather than proximally, are common on the flagellar shaft in Solpugidae (pl. 49D–L).

Although the flagellum of Solpugidae is highly sclerotized and immovably attached to the fixed (dorsal) finger, it remains flexible. Sørensen (1914: 165) identified a section of pliable dorsal cuticle, situated slightly distal to a section of pliable ventral cuticle, at the base of the flagellar shaft of *Zeria keyserlingi* (Pocock, 1895). Similar flexible sections of cuticle observed in the present study, e.g., in *Solpugema genucornis* (pl. 49B, arrow), suggest a point of "articulation" during the forward projection of the flagellum caused by hemolymph pressure during copulation. Sørensen's (1914: 165) reference to "articulation" of the flagellum of Solpugidae therefore does not imply an ability to rotate within a socket, but to the flexibility of the shaft itself. A dorsal carina on the bulbous base of the flagellum, referred to as the **bulbous base carina** (fig. 25), may prevent the base from yielding under hemolymph pressure, ensuring that pressure is distributed into the shaft, and in turn causing it to project distally (Sørensen, 1914: 168). A suture on the prolateral side of the base that extends approximately parallel to the carina, may be the site of longitudinal infolding of the seta from which the flagellum was derived. Sørensen (1914: 171, 172) suggested that the size of the bulbous base may be correlated with the length of the shaft, but no such correlation was evident in the material examined for the present study.

Two lumens extend through the flagellum (pl. 41E). The alembic lumen comprises an alembic canal, terminating basally in an alembic pouch that is often visible through the cuticle of the base, and opening apically on the shaft to the exterior. The blind-ending hemolymph lumen is connected basally, via the atrium, to the hemolymph in the fixed finger (Lamoral, 1975). The atrium (Sørensen, 1914: 168, fig. 11, labeled "c") is a longitudinal space situated ventral to and separated from the lumen by a chitinous membrane (Roewer, 1934) comprising dorsal and ventral lamellae extending longitudinally, and apparently functioning together as a valve that opens under strong hemolymph pressure but prevents backflow. This mostly unidirectional valve may allow the flagellum to retain pressure in the shaft even after the muscles that cause the hemolymph to move into and remain in the shaft have ceased contracting. Roewer (1934: 154, fig. 156, reproduced here as fig. 22D) provided a cross section of the bulbous base whereas Lamoral (1975) provided longitudinal sections of the base and cross sections of the shaft, based on histological investigations.

Subspiniform to spiniform setae associated with the flagellum (*fcs*) are absent in Solpugidae. Setal modifications on the prolateral surface of the chelicera are limited to slightly more differentiated plumose setae (flagellar complex plumose setae, or *fcp*) near the bulbous base (pl. 45B), and/or toward the apex of the fixed (dorsal) finger, e.g., in *Oparba asiatica* (pls. 27, 45D) and *Solpugisticella kenyae* (pl. 124G). The distalmost modified setae on the movable finger are the most robust, gradually becoming less modified proximally. Modified fixed finger *pvd* setae may or may not exhibit remnants of plumosity.

Summary of the Flagellar Complex

A cheliceral flagellum is restricted to adult males and present in all suprageneric taxa except Lipophaginae, some Eremobatidae and some Melanoblossiinae. Two flagella, a primary and secondary flagellum, are present in Rhagodidae and at least two genera of Karschiidae (*Barrussus* and *Eusimonia*). They are situated close together, forming a diploflagellum, in Rhagodidae. The primary flagellum may be defined as a modified ventral flagellar seta, and the secondary flagellum as a modified dorsal flagellar seta. Three types of primary flagella may be identified: setiform, sessile, and composite. Composite flagella comprise a stalk, base and, often, a shaft.

Flagella or homologs thereof may be immovably fixed (Ammotrechidae, Dinorhaxinae, Eremobatidae, Gylippinae, Karschiidae (excluding *Karschia*), Lipophaginae, Melanoblossiinae, Mummuciidae, Rhagodidae, and Solpugidae) or rotatable paraxially (Ceromidae, Daesiidae, Hexisopodidae, and *Karschia*) or subdiaxially (Galeodidae). In the resting position, the apex of the flagellum or its homolog may be directed distally (Ammotrechidae, Eremobatidae, Gylippinae, Lipophaginae, Melanoblossiinae, and Mummuciidae), distodorsally (Rhagodidae and Karschiidae, excluding *Karschia*), proximally (Ceromidae, Daesiidae, Hexisopodidae, Solpugidae), dorsoproximally (Galeodidae), or ventrally (Dinorhaxinae). All rotatable flagella are thus proximally directed and fixed flagella distally directed except for Solpugidae, which are proximally directed. Although the flagellum of Solpugidae is fixed to the finger, it can probably be projected distally by hemolymph pressure and an “articulation point” at the base of the shaft (Sørensen, 1914), or along it (pl. 49B).

Various cheliceral processes and modified flagellar complex plumose (*fcp*) setae and flagellar complex subspiniform to spiniform (*fcs*) setae may be associated with the flagellum. Together with the flagellum, such modified setae form a flagellar complex. These include a fanlike cluster of stiff, often pipette-shaped *fcp* setae at the base of the flagellum, characteristic of Ceromidae, a distinct plumose *fcp* seta and one to four robust spiniform *fcs* setae near the point of attachment of the flagellum of Galeodidae, and one or two dorsally situated subspiniform (in Karschiidae) to spiniform (in Ceromidae and Gylippinae) *fcs* setae. Modified plumose setae become increasingly modified the more distally situated on the fixed (dorsal) finger, e.g., the increasingly longer plumose setae of *Karschia* and the more robust *pvd* setae near the apex of the finger of some Solpugidae. Cheliceral spines are rare in solifuges, but, when present, form dorsal hornlike processes or toothlike cheliceral spines, especially in Karschiidae, but also in some Daesiidae (e.g., *Ammotrechelis goetschi*) and Lipophaginae (e.g., *Trichotoma michaelseni*).

A setiform flagellar complex (*sfc*) is a type of flagellar complex which comprises a distinctly differentiated cluster of modified setae situated apically (Eremobatidae and Lipophaginae) or prolaterally (Melanoblossiinae) on the fixed finger. All setae in the complex, including the flagellum, if present, are setiform in appearance. Three types of setiform flagellar complex, i.e., *type A* (Eremobatidae), *type B* (Lipophaginae) and *type C* (Melanoblossiidae) are recognized, based on the origin of the modified setae (*pdd*, *pvd*, etc.), and the arrangement and position of the setal cluster on the fixed (dorsal) finger.

The function of the male flagellum remains uncertain, and several possibilities are suggested in the present contribution. The only unequivocal observation of a flagellum apparently functioning as an intromittent organ, with the cheliceral fingers not handling the sperm during indirect sperm transfer, is the bowl-shaped flagellum of Ammotrechidae. During flagellar insertion in the female genital tract, alembic fluid appears to be secreted by all whiplike flagella through a pore at the apex. The species-specific nature of the flagellum of many families will remain difficult to explain until more observations of mating behavior, studies on female genital tract morphology and on details of flagellar microstructures (spicules, etc.) and intraspecific variability thereof, become available.

CONCLUSIONS

The enormous chelicerae relative to body size is the most prominent feature of the arachnid order Solifugae. The chelicerae of solifuges, especially the adult males, are particularly rich in characters. Except for the tarsal setae and the number of tarsomeres, almost the entire foundation of solifuge systematics is based on cheliceral characters. In most solifuge families, species delimitation is based primarily on cheliceral dentition and the male flagellum, yet no comprehensive survey of these character systems has ever been undertaken. Terminology has remained unstandardized, confusing, and even contradictory. The poor understanding of cheliceral characters, together with the unsatisfactory terminology applied to them, has hindered the systematics of Solifugae, compared to other arachnid orders, e.g., Araneae, the major character systems (e.g., eye patterns, male pedipalp, spinnerets; Ramírez, 2014) of which are well understood and described with a unified terminology. The present study is the first comprehensive synthesis of solifuge cheliceral morphology that attempts to homologize cheliceral characters across the order based on a survey of exemplar species representing all major solifuge lineages.

This survey of the chelicerae discovered many novel characters, e.g., the movable finger fondal (*mff*) setae, the mucron organ (mo), and the medioventral organ (mvo). Many other characters were reinterpreted, e.g., the fused hornlike process previously interpreted as a large tooth in the lipophagine, *Trichotoma michaelseni*. Numerous potential suprageneric synapomorphies were identified, including broad patterns in taxonomically restricted character systems, such as the stridulatory apparatus, and ubiquitous character systems, such as dentition.

Identification of the homologs of individual teeth, including the first hypotheses regarding fondal teeth, facilitated the discovery of patterns, e.g., direction of size gradation in categories of secondary teeth, and the evaluation of intraspecific variation, justifying the use of dentition in solifuge systematics. Solifuges were found to possess a relatively high propensity for intraspecific variation in dentition, but such variation was largely restricted to predictable areas. For example, the secondary teeth and the fondal teeth were more variable than the primary teeth and the distal teeth usually more variable than the proximal teeth, especially among the primary teeth. Particular fondal teeth were more prone to variation. The shape of teeth was conserved in some species, but not others.

Terminology for cheliceral chaetotaxy was completely overhauled by distinguishing between different series and fields of setae, including the male flagellum, a highly modified seta that manifests a diversity of forms, and is unique to solifuges. The concept of primary and secondary male flagella was introduced. The distalmost seta in the proventral distal (*pvd*) series, i.e., the ventral flagellar seta (*vfs*), was hypothesized to be the precursor to the primary flagellum and the distalmost prodorsal distal (*pdd*) seta, i.e., the dorsal flagellar seta (*dfs*), the precursor to the secondary flagellum.

A single origin was hypothesized for the primary flagellum, but alternative interpretations were proposed for further testing, and areas requiring more investigation were identified, notably the homology of the setae hypothesized to be the flagellum and the *sfc principal seta* in Melanoblossiinae. The terminology for the primary flagellum was standardized and three types, i.e., setiform, sessile, and composite, identified. Components of the composite flagellum, i.e., the stalk, base, and shaft, were homologized.

The present contribution has broad implications for solifuge systematics and evolutionary biology. It increases the number of characters from species to family level, and provides a new framework for taxonomic and phylogenetic studies on the order in the form of revised terminology and character definitions. It is the first study to propose hypotheses of primary homology for phylogenetically and taxonomically useful cheliceral structures across Solifugae, observations that can be coded into characters and tested for secondary homology in phylogenetic analyses, providing synapomorphies for the higher classification of the order (work in preparation by the authors).

The literature on behavior and functional morphology of the chelicerae of Solifugae was reviewed and interpreted in light of the present study. The conserved female chelicera, with its robust shape and putatively plesiomorphic dentition and chaetotaxy (including increased plumosity of the *pvd* setae), appears to reflect its primary functions for feeding and probably defense. Sexually dimorphic modifications of the male chelicerae, e.g., gracile shape, modified, often reduced dentition, modified setae forming the flagellar complex, and, in most species, the flagellum itself, function in mating. Mating behavior in solifuges was divided into three phases, i.e., somatic contact, genital contact, and release phases, and the relevance of cheliceral modifications to each phase was discussed. Increased standardization and more detailed description of mating behavior, studies on the internal anatomy of the female reproductive system, and histological studies of the male flagellum are needed to improve understanding of the function of cheliceral modifications in solifuge mating.

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APPENDIX 1

Glossary of Terminology

Terms in languages other than English are in italics. Direct translations are in square brackets.

A/CP ratio: Ratio indicating size of body appendages (A = sum of pedipalp, leg I, and leg IV lengths) to body length (CP = length of chelicera plus length of propeltidium) (fig. 5F; Brookhart and Muma, 1981; Muma and Brookhart, 1988).

alembic canal: See alembic lumen.

alembic lumen (al): Lumen in shaft of flagellum (pls. 32B–G, 41E–N), hypothesized to occur in all flagella with a shaft, including broad shaft of the daesiid, *Ammotrechelis* Roewer, 1934; open externally; lined by epicuticle hence hypothesized to have formed by longitudinal invagination of seta (Lamoral, 1975: 138, fig. 1); function unknown. In Solpugidae Leach, 1815, comprises alembic canal in flagellar shaft that terminates proximally in blind pouch, i.e., alembic pouch (basal pouch sensu Lamoral, 1975); transition from pouch to canal flask shaped (hence alembic), visible through cuticle of bulbous base of flagellum (pls. 32G, 33K, L, 45A). Alembic pouch may be absent outside Solpugidae, equating alembic lumen with alembic canal. No connection between alembic canal and hemolymph. Historical Use: alembic lumen (Lamoral, 1975).

alembic pouch: See alembic lumen.

alveolus: Deep flagellar socket in Galeodidae Sundevall, 1833, *Karschia* Walter, 1889 (Karschiidae Kraepelin, 1899), and Rhagodidae Pocock, 1897 (pl. 40A–C).

anterolateral propeltidial lobe: Lateral lobes partially or entirely fused to propeltidium (Pls. 1A, 3A, B) in Ammotrechidae Roewer, 1934, Ceromidae Roewer, 1933, some Daesiidae Kraepelin, 1899 (e.g., *Ammotrechelis*, *Namibesia* Lawrence, 1962, *Biton* Karsch, 1880), Eremobatidae Kraepelin, 1901, Galeodidae, Karschiidae, Melanoblossiinae Roewer, 1933, Mummuciidae Roewer, 1934, and Solpugidae, but completely separated from propeltidium in some Daesiidae (e.g., *Hemiblossia* Kraepelin, 1899), Dinorhaxinae Roewer, 1933, Gylippidae Roewer, 1933, Hexisopodidae Pocock, 1897 (but see Roewer, 1934: 42; Muma, 1976), and Rhagodidae (based on Muma, 1976; Wharton, 1981); each lobe bears anterolateral cheliceropeltidial articulation (anterolateral chelicerocarapacal articulation sensu Shultz, 1990) and lateral eyespots (Bernard, 1894). Similar articulation present in Pseudoscorpiones De Geer, 1778, except for some species of superfamily Chthonioidea Daday, 1888 (Chamberlin, 1931; Shultz, 1990). Pocock (1893) misinterpreted as basal sclerite of chelicera, hence argument for three-segmented chelicera in Solifugae, but presence of eyespots indicates "carapacal" origin (Shultz, 1990: 11). Historical Use: buttress to which the mandible is articulated [on each side of the head] (Pocock, 1900b: 133); *Lobus exterior* [exterior lobe] (Roewer, 1934; Muma, 1976; Wharton, 1981); lateral lobe (e.g., Carvalho et al., 2010).

asetose areas: Distinct areas devoid of setae and more sclerotized than surrounding areas (Pls. 1B, C, 4); usually dark reddish brown; includes fixed finger terminal tooth (FT), movable finger terminal tooth (MT), area extending along gnathal edges of fingers and teeth, stridulatory plate, pro- and retrolateral interdigital condyli (pic and ric), cheliceropeltidial condyli (cpc), ventral digital plagula (vdp), and ventral manus plagula (vmp) (pls. 3, 6A). Historical Use (relevant only to asetose areas of fingers): hardened points of digit (Bernard, 1896: 323); *besonders dicker Chitinregionen* (Roewer, 1934: 118).

atrium: Narrow, longitudinal "chamber" of hemolymph below bulbous base of flagellum in Solpugidae (fig. 22D); connected to hemolymph lumen of base through longitudinal valve, extending along base of bulb. Not mentioned by Lamoral (1975) in histological investigation of Solpugidae flagellum. Historical Use: *atrium* (Sørensen, 1914).

basal cheliceral apodeme: Collarlike ingrowth of exoskeleton at base of chelicera at articulation with propeltidium (pl. 3D–I); forms rim of basal cheliceropeltidial foramen; separated from external cheliceral surfaces by cheliceropeltidial articular membrane (cpam); site of cheliceral muscle attachment (Roewer, 1934: 52; Van der Meijden et al., 2012). Historical Use: *Chitinwulst-Umrandung* [chitinous lipped rim] (Roewer, 1934: 52, fig. 47, 55); basal ring [but apparently in broader sense than used in present contribution] (Van der Meijden et al., 2012).

basal fondal margin: Basal margin of strongly sclerotized, asetose fond (fig. 2A). Historical Use: edge of mandibular joint (Birula, 1926: 196); *Gelenksrande* [margin of joint] (Birula, 1937a); socket margin of movable finger (Muma, 1951: 39, 43).

basal peg: Swelling at "base" of flagellum of *Karschia* (Karschiidae) (pl. 40C); may be homologous to base of composite flagellum and previously suggested to be homologous with base of flagellum of Ceromidae (Roewer, 1934: 148); may prevent movement at "base" during extension of flagellum (Roewer, 1934: 146). Historical Use: *pétite apophyse* [small apophysis] (Sørensen, 1914: plate II, fig. 14); *Zapfen* [spigot] (Roewer, 1934: 142).

basifondal (BF) teeth: Small to minute, but distinct teeth medially on basal fondal margin forming third row of fondal teeth; most pronounced in Galeodidae (pl. 64K, L) and Rhagodidae (pl. 64I, J), present but reduced in some Eremobatidae (pl. 84I, J), absent, signs of vestigial teeth evident, in, e.g., Ceromidae (e.g., pl.

96A, C). Historical Use: *eine dritte Reihe kleiner, aber deutlicher Zähne* (Roewer, 1934: 54); *Gelenksrande sitzenden Zähnchen* (Birula, 1937a).

bifid setae: Apically forked setae (fig. 10A); one of most common setal types in Solifugae, present on retrolateral surface of chelicera, but absent on prolateral surface. Historical Use: *Gabelborsten und Gabelhaare* (Kraepelin, 1901); cleft apically (Hewitt, 1934; Lawrence, 1935).

bulbous base: Swollen base of flagellum of Solpugidae (fig. 25, pls. 32G, 33K–M); immovably fixed dorsally or prodorsally along its length (above atrium) to chelicera; contains alembic pouch. Historical Use: proximal portion of flagellum (Pocock, 1895); basal enlargement of flagellum (Purcell, 1903c: 305); basal lamina of flagellum (Pocock, 1897); *Grundschwiele* (Kraepelin, 1901, 1908a); basal lobe (Hirst, 1911b); *ballon* (Sørensen 1914); basal enlargement (Hewitt, 1919b); *Blase*, *Basalblase des Flagellum* (Roewer, 1934: 154, 444); enlarged ovate to globular base (Muma, 1976); flagellar base, bulbous base (Wharton, 1981).

bulbous base carina: Moderately to strongly sclerotized, smooth to jagged, dorsal to proximodorsal ridge along bulbous base of male flagellum in Solpugidae (fig. 25, pl. 33L); may prevent bulbous base yielding during expansion of flagellum, thus increasing hemolymph pressure (Sørensen, 1914: 168). Historical Use: *carène* [carina] (Sørensen, 1914); *Dorsalrippe* [dorsal ridge of bulbous base] (Roewer, 1934: 153).

callus: Strongly sclerotized, lobate asetose area on fixed (dorsal) finger of both sexes in Hexisopodidae (fig. 6A; pls. 127C, 128D, E); usually with blunt spines (outgrowths or tubercles). Historical Use: hairless area at base of fang (Purcell, 1899: 384); sclerotized patch (Lamoral, 1973); callus (Wharton, 1981).

chaetotaxy: Arrangement, nomenclature, and classification of setae (Gordh and Headrick, 2001), e.g., pls. 12–14; pending further study, cuticular processes pertaining to chelicera here categorized into spines (rare in Solifugae, vide Lamoral, 1973) and setae (see macrosetae, microsetae, spines, dorsal cheliceral spine, and dorsal hornlike process). Historical Use: Kraepelin (1901: 8) defined nine types of setae in Solifugae, i.e., *Dornen* [spines], *Dornenborsten* [spinose bristles], *Borsten* [bristles], *Haare* [hairs], *abgestutzte Borsten* [bristles abruptly narrowing at apex, e.g., stridulatory setae], *Gabelborsten und Gabelhaare* [bifid bristles and hairs], *Cylinderborsten* [cylindrical bristles], *Tubenhaare und Tubenborsten* [ctenidia], *Papillen* [papillae]. All except ctenidia and papillae occur on the chelicera. Roewer (1934: 121) recognized and defined these types as *Dornen* [spines] when shaft inflexible, *Borsten* [setae/bristles] when slightly flexible, *Haaren* [hairs] when very flexible, and *ctenidien* [ctenidia] and *papillae* [papillae] when unsclerotized. El-Hennawy (1998: 6, fig. 5) largely followed Kraepelin's (1901) distinction among spines, bristles, spinous-bristles, and sense hairs. Lawrence (1956: 120) used translations "spinose setae" (for *Dornenborsten*) and "spines" (for *Dornen*) to refer to different setae but, in discussion on rhagodid taxonomy, emphasized that it is often impossible to assign setae to one category or another, and hence often used spinelike setae for those not rigid enough to be referred to as spines (Lawrence, 1956: 129). Lamoral (1973) noted correct definition of "spine" is outgrowth of cuticle, whereas "seta" is outgrowth of epidermis with some flexibility and connected to cuticle by means of membrane. Lamoral (1973) noted true spines rare in Solifugae, rejected use of "spine," and suggested use of "spinelike" setae for rigid setae, a suggestion followed by some (e.g., Muma, 1976; Wharton, 1981) but not all (e.g., Maury, 1985; Gromov, 2003b; Reddick et al., 2010; Cushing and Castro, 2012) subsequent workers.

chelicera (-ae): First pair of appendages in Chelicerata (fig. 1, pl. 1); large, two-segmented, and chelate in Solifugae, first (basal) segment comprising manus and fixed (dorsal) finger, second (terminal) segment referred to as movable (ventral) finger. Historical Use: *Fangscheeren* [scissors fang] (Pallas in Lichtenstein and Herbst, 1758); *mandibules en pinces* (Latreille, 1796: 188); *de forcipules* [claspers] (Savigny, 1809: 176); *antenne-pinces* [antennal clamps] (Latreille, 1829: 212); *chélicères* (Latreille, 1829: 212);

Fresszangen [fang scissors] (Koch, 1842); chela (Hutton, 1843); *mandibules* (Blanchard, 1847; Dufour, 1861: 348; Pavesi, 1897); mandibles (Putnam, 1883: 257; Pocock, 1895; Purcell, 1899; Hewitt, 1914a, 1919b; Lawrence, 1927); chelicera (Pocock, 1889; Heymons, 1902; Hewitt, 1914a, 1919b; Panouse, 1960b); *Kiefer* [jaw]/*Oberkiefer* [maxilla] (Kraepelin, 1899); *Mandibeln* (Mdb) (Kraepelin, 1901: 5; Heymons, 1902; Birula, 1916, 1937a); *les antennes*/"*chélicères*" (Sørensen, 1914: 158); *Cheliceren* (Roewer, 1934: 53; Lamoral, 1975); *queliceros* (Maury, 1970).

cheliceral fingers: On chelicera, two opposable, distal digits, bearing teeth (pl. 1), i.e., fixed (dorsal) finger and movable (ventral) finger. Historical Use: See table 5.

cheliceral mill: Behavioral term referring to combination of movements made by chelicerae and cheliceral fingers during feeding (e.g., Muma, 1966c); involves scissorslike movements of cheliceral fingers, and forward-backward, up-and-down movements of entire chelicerae, presumed to grind food between stridulatory ridges.

cheliceropeltidial articular membrane (cpam): Membrane around cheliceral foramen (pls. 1A, 3A) that connects chelicera to prosoma. Historical Use: *la membrane conjonctive* (Sørensen, 1914); *prosomalen Pleura*, *pl* (Roewer, 1934: 52, fig. 47); flexible membrane (Dunlop, 2000); connective membranes (Van der Meijden et al., 2012).

cheliceropeltidial condyle (cpc): Condyle at proximal end of chelicera (pl. 3C–I); articulates with prosoma to form anterolateral cheliceropeltidial articulation in anterolateral propeltidial lobe of prosoma (Roewer, 1934: 32). Historical Use: *condyle* (Sørensen, 1914: 158); *hintere Apophyse* [posterior apophysis] (Roewer, 1934: 52, fig. 47).

cheliceropeltidial foramen: Rounded-triangular proventral-basal opening on chelicera where attaches to prosoma through cheliceropeltidial articular membrane, and articulates with prosoma through cheliceropeltidial condyle (pl. 3D–I). Historical Use: *une cavité articulaire*...[termed] *un segment de surface sphérique* (Sørensen, 1914).

CH/FFH (cheliceral height/fixed finger height) ratio: Ratio indicating height of fixed (dorsal) finger relative to height of paturon (fig. 5I); previously applied only to taxa with abrupt narrowing of finger, i.e., *Eremobates* (Eremobatidae) males. Historical Use: cheliceral width/fixed finger width (CW/FFW, CW/WFF) (Brookhart and Cushing, 2004).

CL/CH (cheliceral length/cheliceral height) ratio: Aspect ratio, indicating length relative to height of paturon (fig. 5D); one of two measures indicating relative volume of paturon. Historical Use: jaw index (jaw length/jaw breadth) (Cloudsley-Thompson, 1961); L/W (length/width) (Brookhart and Muma, 1981).

CL/CW* (cheliceral length/cheliceral width) ratio: Ratio indicating length relative to width of paturon (fig. 5E); one of two indices measuring volume of paturon. Asterisk indicates width as defined in present contribution, following Maury (1980a) and Botero-Trujillo (2014).

composite flagellum: Flagellum comprising stalk, base, and shaft (e.g., pl. 33), although some components may be secondarily lost; able to change direction and/or shape, probably by hemolymph pressure (Sørensen, 1914: 167, 169; Roewer, 1934: 135–155; Lamoral, 1975); all three sections (stalk, base, and shaft) present in flagellum of Ceromidae, some Daesiidae (*Ammotrechelis*, *Namibesia*, *Syndaesia*), Hexisopodidae, and Solpugidae (e.g., pls. 32A–G, 33A–H, K–M; table 16); shaft or homolog thereof hypothesized to be absent in bowl-, husk-, or vesicle-shaped composite flagella of Ammotrechidae, some Daesiidae (e.g., *Biton*), and some Mummuciidae; base and stalk hypothesized to be absent in Gylippinae (pl. 32H, 33I, J); modification from original setal form may involve longitudinal invagination, at least in some; if shaft present, contains alembic lumen.

condyle: round, strongly sclerotized process by which fixed (dorsal) finger articulates into socket (pl. 2A) with movable (ventral) finger (interdigital condyli, or pic and ric; pls. 1B, C, 2), and chelicera with anterolateral propeltidial lobe (cheliceropeltidial condyle, cpc; fig. 3, pl. 1A).

coxal gland nozzle (cgn): Triangular, anterodorsally directed structure associated with pedipalpal coxal gland; situated dorsally on pedipalpal coxa (pl. 7). Excretory pore of coxal gland opens dorsally on base of nozzle (Alberti, 1979: 51, fig. 2). Historical Use: nozzle (Buxton, 1913: 253); *Mündungsapparat* (Roewer, 1934: 192; Alberti, 1979).

coxal gland nozzle seta/e (*cgns*): Anteriorly to anterodorsally directed seta/e situated at apex of coxal gland nozzle; single seta in most taxa (pl. 7A, C, D), rarely more, usually fewer than five (pl. 7B).

coxal gland setae (*cgs*): Anteriorly to anterodorsally directed setae situated on pedipalpal coxa, directly distal to coxal gland nozzle; usually four to seven (pl. 7).

cuticular canals: Narrow canals approximately perpendicular to axis of finger, extending to cuticular surface, often clearly visible through cuticle of asetose areas of fingers; some appear to terminate in granules (pl. 5A).

dental formulae: Formulae used to describe solifuge dentition; two types, i.e., dental pattern formula (tables 9, 10) describing pattern of dentition, and size-grading formula, usually applied only to fondal teeth (e.g., Maury, 1982), but sometimes to median series and fondal teeth (e.g., Xavier and Rocha, 2001).

dental papillae: Papillae situated prolaterally on chelicera of male *Gylippus* (*Anoplogylippus*) Birula, 1913 (Gylippinae Roewer, 1933), at base of teeth on fixed (dorsal) finger (Birula, 1938: 93, 96, figs. 64, 61); may be simple (*zp.a* – *einfachen* sensu Birula, 1913: 329, fig. 8a) or comb shaped (*zp* – *kammförmigen* sensu Birula, 1913: 329, fig. 8b). Historical Use: *Zahnpapillen* [dental papillae] (Birula, 1913; *pa* in Birula, 1938: 93, 96, fig. 61, 64).

denticles: Minute teeth (figs. 19, 20, arrows) often variable in presence/absence. Historical Use: denticles/denticules (Muma, 1951); granules/granuliform (Lawrence, 1962a, 1962b, 1965b). Birula (1926) used denticles as synonym for teeth.

diploflagellum: Compound structure comprising primary and secondary flagella in male Rhagodidae; superficial appearance of single structure (pls. 30F, 31D). Historical Use: flagellum (e.g., Roewer, 1934); bifid flagellum (Cloudsley-Thompson and Constantinou, 1984).

dorsal cheliceral spine: Proximodorsally to dorsally projecting, apically pointed spine in males of some Daesiidae and *Karschia* (Karschiidae). In the daesiid, *Biton* (*B.*) *gariesensis* (Lawrence, 1931): pointed tooth directed slightly outward (Lawrence, 1931: 134, fig. 3b). Historical Use: *Horn* or *processus rostralis* (Roewer, 1934: 291; Birula, 1935b: 302, fig. 2); *r*, *rh* (Birula, 1938: 44, 50, 58, 60, figs. 18, 24, 34, 36).

dorsal crest: Pronounced, round to angular margin (crest) on fixed (dorsal) finger; common among immatures and adults of both sexes in Ammotrechidae (Muma, 1951: 126, figs. 273, 274; Maury, 1982: 141, figs. 36, 44), immature Ceromidae, some Daesiidae, e.g., *Hemiblossia* (pl. 139G, H), and Mummuciidae (pls. 149E–H, 151C, D, 152B, C); generally more angular in females; in males with bowl- or vesicle-shaped flagella, probably functions to protect flagellum. Historical Use: dorsal keel (Botero-Trujillo, 2014); dorsal hump [referring to angular part of crest in females] (Iuri et al., 2014: 21; Botero-Trujillo, 2014: 321, 325, figs. 11, 17).

dorsal flagellar seta (*dfs*): Apicalmost seta of prolateral dorsal distal (*pdd*) series, situated directly dorsal or proximodorsal to ventral flagellar seta (*vfs*) (pls. 12A, 13, 46C, 47); hypothesized precursor to secondary flagellum in Rhagodidae and most Karschiidae (*Barrussus* Roewer, 1905, and *Eusimonia* Kraepelin, 1899).

dorsal hornlike process: Hornlike process situated dorsally on fixed (dorsal) finger in males of some karschiids, i.e., *Barrus* Simon, 1880, *Barrussus*, *Eusimonia* (dorsodistally projecting process, e.g., pls. 30D, 31B), some Daesiidae (distally projecting process, e.g., pls. 32F; Lawrence, 1931: 134, fig. 3a, b), and the lipophagine, *Trichotoma michaelseni* (Kraepelin, 1914) (distally projecting process fused dorsally to fixed finger, e.g., fig. 6E, pls. 87A–D, 88C). Historical Use: *Ammotrechelis* (Daesiidae): anteriorly projecting dorsal process (Muma, 1971). *Eusimonia* (Karshiidae):

crochet fixe, *profondément bifurqué* (Simon, 1879: 128, 129); *Horn* or *Hornfortsatz* (Kraepelin, 1901: 140, 1908a); horn (Hirst, 1908); dorsal process of immovable finger (Hirst, 1910); *Horn* or *Processus rostralis* (Birula, 1935a: 1218); *Gabelhaken des Chelicerenfingers* or *Chelicerenfingergabel* (Roewer, 1934: 143, 144); dorsal cheliceral horn (Muma, 1976: 6); *Finger ist gegabelt* (Pieper, 1977); forked appendage of dorsal cheliceral finger (Gromov, 2000: 82).

external cheliceropeltidial condylar attachment (ecpca): Pale area visible on anterolateral propeltidial lobes (pls. 1A, 3A, B); external indication of where condyle is attached inside lobe; barely visible to very distinct.

fang: Obsolete term, common in older literature. Historical Use: Often synonymous with movable finger (e.g., Pocock, 1893: 10: "terminal segment [movable finger] or fang") or teeth (Pocock, 1895: 84). Most common usage describes dorsal finger (usually as "upper fang") or some more distal part of dorsal finger (usually as "terminal fang"). Terminal fang usually synonymous with mucron (e.g., Purcell, 1899: 384; Pocock, 1900b: 133; Hewitt, 1921, 1923) but limits arbitrarily defined. In Hexisopodidae, "fang" refers to toothless or apparently toothless section of finger, callus or denticular ridge at flagellar base indicated to be at base of fang (Purcell, 1902; Lamoral, 1972). Also often used to describe part of dorsal finger distal to fondal teeth (Lawrence, 1928: 262, in reference to median series as "fang series"), especially in modified chelicera where refers to larger toothless areas (e.g., Purcell, 1899: 394, in a modified daesiid chelicera). Not always restricted to toothless areas. "Basal portion" of fang described to "commence at first [distalmost] tooth of inner series [profondal row]" in the ceromid, *Toreus capensis* (vide Purcell, 1899: 100). Although neither Purcell (1899) nor Hewitt (1921, 1923) defined "fang," extent thereof apparent from their usage. For example, Hewitt (1921: 9) described "terminal fang of lower jaw strong, the distance from its tip to the tip of the first tooth scarcely 1¼ times the distance between the first and third teeth" and Hewitt (1923: 56) described dentition on fixed finger as "with two large teeth in front, behind the long terminal fang." These distances are measured from apex of movable finger medial (MM) tooth to tip of finger (e.g., Hewitt, 1919b: 31).

fixed (dorsal) finger: Distal part of first (basal) cheliceral segment (paturon) (pl. 1A). Fixed (dorsal) finger possesses two basal condyli, viz. the prolateral (pic) and retrolateral (ric) interdigital condyli (fig. 2, pl. 1B, C), responsible for articulation of fingers relative to each other (see manus for division between manus and fixed finger). Birula (1937a) divided fixed finger of galeodids into *Endteil*, toothless area distal to median row of teeth, or mucron, and *Basalteil*, measured from distal end of median series of teeth to insertion point of flagellum, approximately between fixed finger medial (FM) and fixed finger proximal (FP) teeth. Historical Use: See table 5.

fixed finger basal notch: Broad notch at base of finger visible in dorsal view; in eremobatid species belonging to *scaber* group of *Eremobates* (Muma, 1951; Brookhart and Cushing, 2004: 285, fig. 1). Historical Use: basal notch (Muma, 1951: 51).

fixed finger crimp: Slight to marked upturn in largely styletlike fixed (dorsal) finger of Eremobatidae (pl. 67A, arrow). Historical Use: crimp (Brookhart and Cushing, 2004: 294, fig. 31).

fixed finger distal (FD) tooth: Distalmost primary tooth on fixed (dorsal) finger and thus also distalmost tooth on finger (pls. 21, 22A–D; table 6), but see multidentate taxa and discussion of daesiid dentition. Historical Use: *dent distale* (*dd*) [distal tooth] (Vachon, 1950: 101, fig. 13); *première dent antérieure* (*DA1*) [first anterior tooth] (Panouse, 1956: 212); anterior tooth (e.g., Muma, 1951; Lawrence, 1968). On fixed finger, anterior teeth often used by various authors as encompassing distal and medial teeth as well as secondary teeth situated between them, e.g., *Vorderzähne* [anterior teeth] (Kraepelin, 1899, 1901; Roewer, 1934: 53); *dent antérieure* (Panouse, 1960b: 176, fig. 2); *anterior* (*A*) (Maury, 1982, 1984); anterior teeth (Martins et al., 2004); anterior teeth, as Fa_1, Fa_2, Fa_3 (Botero-Trujillo, 2014). Muma (1951: 38, fig. 5) distinguished between two distalmost primary teeth on fixed finger, referred to more proximal thereof as "medial tooth" (MT), and to teeth situated between them as "intermediate teeth," a term previously restricted to fixed finger submedial (FSM) teeth.

fixed finger medial (FM) tooth: First primary tooth distal to proximal tooth on fixed (dorsal) finger (pls. 21, 22A–D; table 6; Muma, 1951); putative serial homolog of movable finger medial (MM) tooth. HISTORICAL USE: Usually referred to as one of anterior teeth, e.g., *seconde dent antérieure* (*DA2*) [second anterior tooth] (Panouse, 1956: 212); medial tooth (MT) (Muma, 1951). Kraus (1966: 183, figs. 1–4) labelled both fixed finger medial (FM) and fixed finger submedial (FSM) teeth as *Zwischenzähne* [intermediate teeth].

fixed finger proximal (FP) tooth: Proximalmost primary tooth on fixed (dorsal) finger (pls. 21, 22A–D; table 6); often largest tooth on fixed finger; putative serial homolog of movable finger proximal (MP) tooth. HISTORICAL USE: *Hauptzahn* [main tooth] (Kraepelin, 1899, 1901; Roewer, 1934: 53); chief tooth (Birula, 1926); terminal tooth of fang series (Lawrence, 1928: 262); *dent principale* (*DP*) [principal tooth] (Vachon, 1950; Panouse, 1956, 1960b); principal tooth (Muma, 1951; Brookhart and Cushing, 2002); main tooth (Turk, 1960; Van der Meijden et al., 2012); main basal tooth (Wharton 1981: 69); *principal* (*P*) (Maury, 1984); central tooth (El-Hennawy, 1998); primary tooth (Brookhart and Cushing, 2004; Catenazzi et al., 2009); posterior tooth (Bayram et al., 2011); principal tooth, as *Fp* (Botero-Trujillo, 2014).

fixed finger subdistal (FSD) tooth/teeth: One or more secondary teeth situated between fixed finger medial (FM) and fixed finger distal (FD) teeth (pls. 21, 22A, D; table 6).

fixed finger submedial (FSM) tooth/teeth: One or more secondary teeth situated between fixed finger proximal (FP) and fixed finger medial (FM) teeth (pls. 21, 22A–D; table 6). HISTORICAL USE: Usually referred to as intermediate tooth/teeth on fixed finger (e.g., Kraepelin, 1899, 1901; Roewer, 1934: 53; Panouse, 1960b: 176, fig. 2; Maury, 1982, 1984; Martins et al., 2004); intermediate teeth, Fi_1, Fi_2 (Botero-Trujillo, 2014).

fixed finger subterminal (FST) tooth/teeth: One or more secondary teeth situated on fixed finger mucron, i.e., between fixed finger distal (FD) and fixed finger terminal (FT) teeth (pl. 158D, F; table 6); uncommon.

fixed finger terminal (FT) tooth: Tip of fixed (dorsal) finger, i.e., distalmost part of mucron (pls. 21, 22A–D; table 6); putative serial homolog of movable finger terminal (MT) tooth. HISTORICAL USE: terminal fang (Pocock, 1895; Purcell, 1899); *Endspitze des Oberfinger* [apex of finger] (Birula, 1937a). Traditionally interpreted either as equivalent to the mucron (e.g., Pocock, 1895), or as a section thereof, e.g., "terminal fang [mucron] of moderate length, the apex [terminal tooth] suddenly and strongly curved downwards…" (Hewitt, 1913: 479). Pocock (1895: 84) was first to treat apex of finger as tooth ("terminal fang") similar to median series teeth ("second and third large fangs of the upper jaws").

flagellar attachment point: Point of attachment of flagellum to fixed (dorsal) finger, or point around which flagellum rotates in socket or modified socket on fixed finger (pl. 40); area through which flagellar lumen, if present, connects with hemolymph in chelicera; fixed (Ammotrechidae, Eremobatidae, Gylippinae, Karschiidae excluding *Karschia*, Melanoblossiidae, Mummuciidae, Rhagodidae, and Solpugidae) or rotatable (Ceromidae, Daesiidae, Galeodidae, and Hexisopodidae and the karschiid, *Karschia*); absent in Gylippinae; inner surface of socket often more strongly sclerotized, especially in Ammotrechidae, Ceromidae (pl. 96A), Daesiidae, Hexisopodidae, Mummuciidae, and *Karschia* (Karschiidae); attachment round to oval in Ammotrechidae and Mummuciidae (pls. 34E–H, 35G, H). HISTORICAL USE: Ammotrechidae: *anillo de fijación* [attachment ring] (Maury, 1982: 136). Daesiidae: *chitinösen Fixationspunkt* (Kraepelin, 1908a: 220); rotatory centre (Lawrence, 1956: 123; 1965a: 55); *kreisrunden Chitinring der Anheftung* or *kreisrunden Anheftungsring* [circular attachment ring]

(Roewer, 1934: 150). Karschiidae: *Basalring* (Roewer, 1934: 146). Mummuciidae: attachment base, attaching ring (Xavier and Rocha, 2001: 129, 132, fig. 10), probably referring to short stalk. Mostly used broadly in literature, with little distinction between inner margin of socket, general reference to "attachment point," and hairpin pattern made by stalk transitioning into base, e.g., "rotatory axis...as an ill-defined longish triangular marking" (Lawrence, 1928: 266, plate XXIII, fig. 48).

flagellar base: In composite flagellum, section of flagellum distal to stalk and proximal to shaft, if present (pls. 32A–G, 33A-H, K–M); swollen capsular structure in Ceromidae, cuplike base in Hexisopodidae and *Namibesia* (Daesiidae), bulbous base in Solpugidae, membranous bowl-shaped base in *Ammotrechelis* (Daesiidae), main membranous structure (i.e., bowl-, husk-, or vesicle-shaped "flagellum") of Ammotrechidae, Mummuciidae, and most Daesiidae; absent in Eremobatidae, Karschiidae (but homology of basal peg of *Karschia* uncertain), Galeodidae, Gyllippidae, Melanoblossiidae, and Rhagodidae. Historical Use: Ceromidae: basal enlargement of flagellum (Purcell, 1899: 395). Solpugidae: See bulbous base.

flagellar complex: In male solifuges, all distinctly modified sexually dimorphic setae on chelicera, all situated apically on prolateral surface of male cheliceral fixed (dorsal) finger except for retrolateral manus spiniform (*rlms*) seta in Gylippinae; includes flagellum, if present, and associated flagellar complex plumose (*fcp*) setae, flagellar complex subspiniform to spiniform (*fcs*) setae, and retrolateral manus spiniform (*rlms*) seta. In Ceromidae, comprises rotatable whiplike flagellum, two or three spiniform (*fcs*) setae, and row of stiff, often pipette-shaped (*fcp*) setae at flagellar base (pls. 32A, B, 33A–C; Roewer, 1934: 147, 1941: 117). In most Daesiidae, comprises rotatable, membranous flagellum and two to four distalmost *pvd* setae, which are slightly more differentiated than more proximally situated *pvd* setae in some *Blossia* Simon, 1880 (pl. 139C). In Dinorhaxinae, comprises nonrotatable filiform flagellum and one to three spiniform setae dorsally and ventrally. In Galeodidae, comprises rotatable, spoon-shaped flagellum, single stout plumose (*fcp*) seta, and one to four spiniform (*fcs*) setae near point of flagellar attachment (pls. 30G, H, 31E, F; Turk, 1960: 109). In Gylippinae, comprises immovably fixed straplike flagellum, one or two flagellar complex spiniform (*fcs*) setae and single retrolateral manus spiniform (*rlms*) seta (pls. 32H, 33I, J). In Hexisopodidae, comprises rotatable whiplike flagellum and prodorsal spiniform setal cluster (*pdsc*) in *Chelypus* (pl. 32C, 33E). In Karschiidae, comprises rotatable, coiled, filiform flagellum, one or two subspiniform (*fcs*) setae near point of flagellar attachment, and suit of similarly or differently modified proventral distal (*pvd*) setae (i.e., *fcp* setae) in *Karschia* (pls. 30A–C, 31A; Panouse, 1955; Roewer, 1934: 144; Pieper, 1977), or fixed ventral (primary) and dorsal (secondary) flagella, and one or two subspiniform (*fcs*) setae near base of cheliceral hornlike process in *Barrussus* and *Eusimonia* (pls. 30D, 31B; Panouse, 1955; Roewer, 1934: 144; Pieper, 1977). In Solpugidae, comprises nonrotatable, usually whiplike flagellum with one to three more plumose (pl. 45C) or slightly thicker (pl. 27) *pvd* setae, i.e., *fcp* setae. When setae, including flagellum, if present, of flagellar complex retain setiform appearance, as in Eremobatidae (pls. 37–39; Muma, 1970a, Brookhart and Cushing, 2004), Lipophaginae Wharton, 1981 (pl. 36A–F), and Melanoblossiinae (pl. 36G–I; Roewer, 1941: 127), flagellar complex referred to as "setiform" (see setiform flagellar complex, or *sfc*). "Flagellar complex" elsewhere equated with flagellum, especially in Eremobatidae and Melanoblossiinae (e.g., Lawrence, 1972: 98; Wharton, 1981: 53; El-Hennawy, 1990: 26; Gromov, 2003b: 199), but not considered synonymous in the present contribution. Historical Use: *zusammengesetzten Natur des Flagellums* (Kraepelin, 1908a: 222); *Flagellumapparatus* [of *Karschia*] (Roewer, 1934: 146); *complexe flagellaire* [of *Eusimonia*] (Panouse, 1955: 347, figs. 2–4).

flagellar complex depression: Prolateral depression in fixed (dorsal) finger, which accommodates setiform flagellar complex of male Melanoblossiinae (fig. 26C, pl. 36G–I). References to "alveoli" in keys of Muma (1976) and Gromov (2003b) appear to refer to sockets of individual setae in setiform flagellar complex (*sfc*) and not to flagellar complex depression.

flagellar complex plumose (*fcp*) seta/e: One or more slightly to distinctly modified proventral distal (*pvd*) setae, situated proximoventral or ventral to point of flagellar attachment in several taxa; differ in shape, robustness, and position relative to flagellar base, but hypothesized to be homologous, modified *pvd* setae. In Ceromidae, smooth (plumosity hypothesized to be secondarily reduced or lost) or plumose, often pipette-shaped *pvd* setae situated in short, closely spaced row at flagellar base (pls. 32A, B, 33A–C). In Galeodidae, stout, plumose seta situated directly proximoventral to point of flagellar attachment (pls. 4C, 30G, H, 31E, F; Birula, 1936a: 48, fig., 1937a, 1937b, 1938; Panouse, 1960b: 178, fig. 4), not obviously connected to *pvd* row (pl. 62A, E, G, I). In Solpugidae, weak to moderately differentiated plumose seta/e situated distal to bulbous base of flagellum (pl. 45B) or robust *pvd* setae near apex (pl. 27). In some *Blossia* Simon, 1880 (Daesiidae), two to four distalmost *pvd* setae slightly more differentiated, but equally so, compared to more proximally situated *pvd* setae (pl. 139C; Hewitt, 1921: 10, fig. 4). In *Karschia* (Karschiidae), plumose setae increasing in length toward flagellum (pls. 30A, 31A, 50A, E), apical one or two setae often more robust or modified into various shapes (see *i*, *f* in Birula, 1938: 58, fig. 34; Gromov, 1998: 181, figs. 1f–I). Historical Use: Ceromidae: radiating tuft of spiniform setae at flagellar base (Pocock, 1897: 254); row of stiff bristles, long stiff feathery hairs that reach to the apex of the fang [in *Ceroma sclateri* Purcell, 1899], row of stiff feathery bristles, which do not…reach the apex of the jaw [in *Ceroma inerme* Purcell, 1899] (Purcell, 1899: 395, 399); fanlike row of feather bristles (Hewitt, 1919b: 23); row of...very stout, smooth, basally expanded spines (Lawrence, 1954: 114); enlarged setae [associated with flagellum] (Muma, 1976: 10; El-Hennawy, 1990: 22); cluster of thickened setae arising from small tubercle (Wharton, 1981: 11). Galeodidae: *hintere gefiederte Borste*, *St.p.* to distinguish from other plumose setae in *pvd* series labelled *vordere gefiederte Borsten*, *St.a.* (Birula, 1937a: 595, fig. 17, 1938: 155, fig. 87). *Karschia* (Karschiidae): *Säbelborsten* (Kraepelin, 1908a); mandible bristles (*i* and *f* in Birula, 1938: 58, fig. 34); dorsal modified setae (Gromov, 1998: 181, figs. 1f–I). Solpugidae: *une grade soie droite plumeuse* (*ibid. s*); *s*, *une soie plumeuse*, *probablement un organe sensitif* (Sørensen, 1914: 173, 212, fig. 10).

flagellar complex subspiniform to spiniform (*fcs*) seta/e: One to five (depending on taxon) subspiniform to spiniform setae, presumably modified prodorsal distal setae (*pdd*), at point of flagellar attachment; part of male flagellar complex; differ in shape, robustness, and position among taxa. In Ceromidae, two or three spiniform setae situated dorsally on chelicera near flagellar base in some species (pls. 32B, 33C); important for species diagnosis. In Galeodidae, intraspecifically variable row of one to four (Birula, 1937a: 594) spiniform setae situated proximoventral to point of flagellar attachment (pls. 4C, 30G, H, 31E, F). In Gylippinae, one or two robust spiniform setae situated prodorsally on chelicera (pls. 32H, 33I, 85A, B); presence/absence and number important for species diagnosis (Birula, 1913). In *Eusimonia* (Karschiidae), one or two subspiniform setae situated dorsally near base of cheliceral hornlike process, e.g., in *Eusimonia furcillata* (Simon, 1872) (pl. 53C, D; Roewer, 1934: 143, fig. 141A) and *E. nigrescens* Kraepelin, 1899 (pls. 30D, 31B). In *Karschia* (Karschiidae), subspiniform setae situated dorsoproximal to point of flagellar attachment; often originating near base of flagellar shaft within spiral formed by flagellum (pls. 30B, C, 31A). Historical Use: Ceromidae: *Oberfingerdornen* (Roewer, 1934: 148). *Karschia* (Karschiidae): *einem dicken*, *gekrümmten Dorn* [hypothesized to keep flagellum in place: *wie von einer seitlichen Klammer*, *in seiner Lage fest gehalten wird*] (Kraepelin, 1901: 145); *spinae flagelli* [flagellar spines] (Roewer, 1934: 291; Lawrence, 1954: 113); spine (*k* and *c* in Birula, 1938: 60, fig. 36). Galeodidae: *Stiftdornen* (Birula, 1905, 1929a: 164, fig. 1); *Dornen unter dem Insertionspunkte des Flagellums* (Birula, 1929b: 276, fig. 2); *Sp - Hinterdornen des Flagellums* (Birula, 1937a: 595, fig. 17, 1938: 155, fig. 87); *Nebendornen* (Birula, 1913: 332, 1937a) [note: Birula (1937a: 593) also used *Nebendornen* to refer to retrolateral manus spiniform (*rlms*) seta of Gylippinae]. Gylippinae: *Fingerdorn*/*Oberfingerdorn* (Birula, 1907; *ofd* in Birula, 1913: 331, fig. 9); *Spina digitalis* [digital spines] (Roewer, 1934: 308); anterior main spine (Lawrence, 1953); a very stout and conical spine (Lawrence, 1954); principal spinelike setae (Wharton, 1981); digital spine (Koç, 2011: 120, fig. 3).

flagellar groove (fg): Prolateral to dorsal groove or longitudinal depression on fixed (dorsal) finger that accommodates male flagellum; different expressions of flagellar groove may or may not be homologous. In Ammotrechidae and Mummuciidae, prodorsal groove on fixed finger, which accommodates flagellum; broad basally, narrowing apically to fit vesicle-, or tapered bowl-shaped flagellum (pls. 34E–H, 35E–I; see González Reyes and Corronca, 2013: 542, fig. 4). In Ammotrechidae, formed by prodorsal and proventral flanges, the former a prolateral curvature of the laterally-compressed dorsal margin of the fixed finger. In Daesiidae, shallow prolateral depression along prodorsal distal margin (pddm) of fixed finger asetose area, which may accommodate flagellum (pls. 139G, 141A; also see Klann and Alberti, 2010: 226, fig. 1A); less distinct than other types of flagellar groove. In Eremobatidae, often well defined, longitudinal, prolateral to proventral groove (pls. 38, 39A–E, H), usually associated with flagellum (see Brookhart and Muma, 1981: 291, figs. 2, 3); may be long (*Eremobates* Banks, 1900; pl. 66C) or short (some *Eremochelis* Roewer, 1934); may be enlarged proximally to form cuplike concavity (pl. 39B); may comprise series of distinct (*bilobatus* group of *Eremochelis*, e.g., pl. 78A) or indistinct (*imperialis* group of *Eremochelis*, e.g., Muma, 1951) creases and folds; carinae (ridges) may be present in groove (pl. 39H); also see ventrodistal concavity. In Gylippinae, shallow dorsal groove in asetose area of fixed finger with which proximal part of flagellum is fused (pls. 32H, 33J). In Solpugidae, prodorsal to dorsal groove in asetose area of fixed finger, in which base of flagellar shaft situated before curving dorsally (pls. 32G, 33K, 48); prolateral margin of groove associated with various proventral to dorsal elongate, jagged, flangelike, or toothlike carinae (flagellar groove processes, FGP) (pl. 20). Melanoblossiinae: See flagellar complex depression. HISTORICAL USE: Eremobatidae: longitudinal groove on median face (Fichter, 1941); mesal groove (Muma, 1951); mesoventral groove (Brookhart and Brookhart, 2006: 301).

flagellar groove process (FGP): Flanges and carinae formed by anterior extension and modification of prolateral rim of flagellar groove in Solpugidae; often associated with mucron organ (mo) (fig. 24B, pl. 20). HISTORICAL USE: e.g., *zahnartig vorspringendem Grat* [toothlike protruding ridge] (Kraepelin, 1901: 64); tooth, keel, ridge (Lawrence, 1929); *Zahnhöcker* or *gezähnelter erhabener Kiel* [toothed, raised keel] (Roewer, 1934: 468).

flagellar hemolymph lumen (hl): Lumen between flagellar membranes (e.g., pl. 30D) or in canal parallel to alembic canal, if present (pls. 32B–G, 41F–N); hypothesized to be connected proximally to hemolymph (through atrium in Solpugidae; Sørensen, 1914); blind ending apically; possibility of hemolymph entering flagellum recognized by Sørensen (1914: 164), Roewer (1934: 135–155) and Lamoral (1975); first histological studies by Lamoral (1975).

flagellar shaft: In composite flagellum, section of flagellum distal to base (pls. 32, 33); usually chitinous and whiplike; present in Ceromidae, some Daesiidae (*Ammotrechelis*, *Namibesia*, and *Syndaesia*), Hexisopodidae and Solpugidae; flagellum of Gylippinae (pls. 32H, 33J) hypothesized to be homolog of shaft, with base and stalk absent; homology with flagellar shaft of *Karschia* (Karschiidae) uncertain. HISTORICAL USE: *partie corniforme* or *corne* [horn] (Sørensen 1914: 165);

shaft (Hewitt, 1919b; Purcell, 1899); *Schaft* (Roewer, 1934: 154); U-shaped crest of the daesiid, *Amacata penai* Muma, 1971, currently in synonymy with *Ammotrechelis goetschi* Roewer, 1934 (Muma, 1971).

flagellar stalk: In composite flagellum, short section of flagellum connecting attachment point on fixed finger to flagellar base (pls. 32C–F, 33D–F, H, 40C, F); facilitates location of flagellum parallel to prolateral surface of chelicera; manner in which stalk transitions to base in many Daesiidae hairpin shaped (pls. 34A, B, 35A, B, 40G–I), e.g., *Biton tenuifalcis* (vide Lawrence, 1962b: 198, fig. 1c); peduncle of flagellum of Galeodidae, references to "stalk" of flagellum in some daesiids, e.g., *Blossia litoralis* (Purcell, 1903a: 5, fig. 3), and Birula's (1935a) use of short *Füsschen,* which attaches dorsal flagellum of *Eusimonia* (Karschiidae) to chelicera, not homologous to stalk as defined here; homology with "stalk" of *Karschia* (Karschiidae) uncertain.

flagellar stem: Stem section of leaflike flagellum in some *Blossia* (Daesiidae) (pl. 145F); often referred to as *stalk* (e.g., Purcell, 1903a: 5, fig. 3), but not considered homologous to flagellar stalk or to peduncle of flagellum of Galeodidae.

flagellar tip: Arbitrarily defined apex of flagellum; may be acuminate, bifid, fringed, etc. (pl. 49D–L); open to exterior in whiplike flagella, e.g., Ceromidae (pl. 41M, arrow), the daesiids, *Ammotrechelis goetschi* (pls. 32F, 33H, arrows; Maury, 1980a: 64, fig. 11) and *Syndaesia mastix* Maury, 1980 (Maury, 1980a: 64, figs. 3, 4), Hexisopodidae (fig. 40G, arrow), Solpugidae (Lamoral, 1975), and perhaps *Namibesia*; usually refers to tip of shaft of sclerotized whiplike flagellum; not homologous to tip of membranous bowl-, husk- or vesicle-shaped flagella (Ammotrechidae, Mummuciidae, and most Daesiidae) as shaft absent and tip refers to tip of base in these flagella.

flagellum, **or male flagellum:** Distinctly modified, strongly differentiated seta, or two setae in Rhagodidae and most Karschiidae (*Barrussus* and *Eusimonia*), originating prolaterally or prodorsally on fixed (dorsal) finger of chelicera (pls. 30–35, 36G, I, 38, 39A–F); present only in adult males. Primary flagellum, assumed to be homologous across Solifugae (pl. 43), derived from apicalmost seta, i.e., ventral flagellar seta (*vfs*) in proventral distal (*pvd*) series (pls 12A, 46A–C, 47). Secondary flagellum, when present, assumed to be homologous in respective taxa, and derived from apicalmost seta in prodorsal distal (*pdd*) series, i.e., dorsal flagellar seta (*dfs*) (pls. 12A, 47). In Rhagodidae, primary and secondary flagella appear to form a single structure, referred to as diploflagellum (pls. 30F, 31D). Flagellum absent in some taxa, notably Lipophaginae (pl. 36A–C) and some Eremobatidae, e.g., *Chanbria regalis* Muma, 1951 and *Eremocosta titania* (Muma, 1951) (pls. 37, 39G–J). If flagellum absent, its putative homolog, an unmodified ventral flagellar seta, presumed to be present. Historical Use: *cirrhe* [cirrus] (Latreille in Dufour, 1861: 428); *un petit appendice mobile* (Savigny, 1816: 178). Gylippinae: Simon (1879: fig. 15) labelled structure now recognized as flagellum as *lamelle transparente* and retrolateral manus spiniform (*rlms*) seta as *flagellum*. *Eusimonia* (Karschiidae): earlier workers (Simon, 1879; Kraepelin, 1901; Hirst, 1908; Birula, 1913; Roewer, 1934: 299; Birula, 1935a) labelled primary flagellum as *flagellum* and secondary flagellum as *Plättchen*, *Lamelle*, or *Bläschenflagellum*, except Kraepelin (1908a) who considered both as "flagellum" (also see table 14); *seta principalis* has also been used for Karschiidae (Birula, 1918; Roewer, 1934: 291). Rhagodidae: references to "flagellum" (e.g., Roewer, 1934: 55, fig. 50) concerned the compound single structure comprising primary and secondary flagella (referred to here as diploflagellum). Primary and secondary flagella referred to as *Stab* [rod] and *Schuppe* [flake], respectively, by Kraepelin (1908a), and plaques by Sørensen (1914: 169). Eremobatidae: single flat bristle of flagellar complex (Fichter, 1941); apical and subapical plumose bristles in *Eremobates* (vide Muma, 1951: 61, fig. 48); apical plumose spine in *Eremorhax* Roewer, 1934 (vide Muma, 1951: 61); apically plumose seta in *Eremothera* Muma, 1951 (vide Muma, 1951); plumose apical bristle (e.g., Muma, 1970a; Brookhart and Cushing, 2002). Melanoblossiinae:

Seta principalis des Flagellum-Komplexes (Roewer, 1941: 1247); flagellum (Purcell, 1903a); *Flagellum* (Roewer, 1941: 127); *appendice mobile* (Savigny, 1809).

FNH/FFH (fondal notch height/fixed finger height) ratio: Ratio indicating height of fondal notch relative to height of fixed (dorsal) finger in Eremobatidae (fig. 5H). HISTORICAL USE: Introduced as fixed finger width/fondal notch width (FF/FN) by Brookhart and Muma (1987), followed by fixed finger width/fondal width (WFF/FW) of Brookhart and Cushing (2002) and later calculated as fondal notch width/fixed finger width (FW/FFW), requiring a switch between numerator and denominator, by Brookhart and Cushing (2004).

FNL/FNH (fondal notch length/fondal notch height) ratio: Ratio indicating dimensions of fondal notch in Eremobatidae (fig. 5H). Fondal length measured across maximum distance; width measured from tip of fondal tooth 1, i.e., apex of retrofondal medial (RFM) tooth to ventral margin of fixed (dorsal) finger (Brookhart and Muma, 1987: 2). HISTORICAL USE: FN ratio (Brookhart and Muma, 1987); LFN/WFN (Muma and Brookhart, 1988: 3, plate 1); FL/FW (Brookhart and Cushing, 2004).

fond: Triangular broadening of base of fixed (dorsal) finger between two diverging rows of fondal teeth (fig. 2A, pls. 2A, B, 22E, F, 64D); derived from *fundus* = base; not to be confused with usage "FW = fond width" (Brookhart and Cushing, 2002), which indicates width of fondal notch, not width of fond. HISTORICAL USE: *fond de la pince* (Simon, 1879: 126, 1880: 402); fond (Putnam, 1883: 257; Fichter, 1941; Muma, 1951, 1970b); *Wangenteil* [cheek part] (Kraepelin, 1901: 99; Birula, 1937a: 568); *Kaufläche* [chewing surface] (Roewer, 1934).

fondal interdigital articular membrane (fiam): See interdigital articular membranes (iam).

fondal notch (FN): Shallow (fig. 2A) to deep (fig. 2B) notch in fixed (dorsal) finger, situated proximal to proximal (FP) tooth in male Eremobatidae (Muma, 1951). HISTORICAL USE: *Basalbuckel* (Roewer, 1934: 570); space between base of dorsal finger and first tooth of fond (Fichter, 1941); fond, fondal notch (Muma, 1951; Brookhart and Muma, 1981, 1987).

fondal series: Diverging rows of small teeth at base of fixed (dorsal) finger, comprising profondal (PF) row and retrofondal (RF) row, which converge toward median series (pl. 22E, F; table 6; Muma, 1951); in addition, basifondal (BF) row on basal fondal margin forms third "row" of teeth (*Gelenksrande sitzenden Zähnchen*, Birula, 1937a) connecting pro- and retrofondal rows into triangle delimiting fond, e.g., in Eremobatidae (pl. 84C, D, I, J), Galeodidae (pl. 64K, L) and Rhagodidae (pl. 64I, J). Basifondal (BF) teeth probably originated as proximal fondal teeth shifted along basal fondal articulation margin, partly based on position of basifondal teeth compared to position of reduced proximalmost profondal (PF) and retrofondal (RF) teeth, e.g., in *Barrussus* (Karschiidae) (pl. 64C, D). Vestigial beadlike teeth of Hexisopodidae (pl. 131) probably reduced fondal teeth, based on larger number of "beads" retrolaterally (more teeth often found in RF row than in PF rows) and similarity to serrated basal fondal margin, e.g., in Eremobatidae (Muma, 1951: 39). Furthermore, distinct fondal teeth often grade into a "denticulate mound" (Wharton, 1981: 42) of indistinct teeth forming ridgelike surface proximally along edge of fondal area. HISTORICAL USE: fondal teeth: *molaires* [molars] (Dufour, 1861); *Wangenzähne* [cheek teeth], e.g., *laterale* (*äussere*) *und mediale* (*innere*) *Wangenzähne* (Kraepelin, 1899, 1901; Roewer, 1934: 58); cheek teeth (translation from German by Turk, 1948; Lawrence, 1962a, 1962b; Levy and Shulov, 1964; Wharton, 1981; El-Hennawy, 1998); double series of teeth, as opposed to "single series," or median series (Hewitt, 1914a: 152); *jugales latérales* and *jugales internes* (Vachon, 1950); *dent jugale* (*DJ*, *DJ int* and *DJ ext*) [cheek teeth] (Panouse, 1960b); *basal externo* (*BE*) and *basal interno* (*BI*) (Maury, 1984); ectal fondal teeth (*Fef*) and mesal fondal teeth ($Fmf_{1–3}$) (Botero-Trujillo, 2014).

gnathal edge: Cutting surface of fixed (dorsal) and movable (ventral) fingers of chelicera; bears median series of teeth. HISTORICAL USE: cutting edge (Botero-Trujillo, 2014).

gnathal edge carina: Distal longitudinal carina situated on gnathal edge; converges with pro- and retrolateral edge carinae toward apex of cheliceral fingers (fig. 6C, pl. 5C); also see prolateral edge carinae and retrolateral edge carinae.

granulations: Small, round structures situated retrolaterally on asetose areas of cheliceral fingers (fig. 8, pl. 5); most prominent on pro- and retrolateral surfaces of movable (ventral) finger where arranged in row from base to apex, grading into pro- and retrolateral edge carinae; with few exceptions (e.g., pl. 5B), less distinct and randomly distributed on fixed (dorsal) finger and toward apex of movable finger. Historical Use: setal pores (Bernard, 1896: 323); granular area (Purcell, 1899: 385); granulations (Lawrence, 1972: 99); presence on prolateral surface mentioned only by Bernard (1896).

interdigital articular membranes (iam): Membranes connecting fixed (dorsal) and movable (ventral) cheliceral fingers at joint, visible proximally adjacent to fond (fondal interdigital articular membrane, or fiam) and ventrally between cheliceral segments (ventral interdigital articular membrane, or viam) (fig. 2B, pl. 2); involved in articulation of fixed and movable fingers (Van der Meijden et al., 2012). Historical Use: *weiche Bindehaut* (Roewer, 1934: 54, fig. 48); less sclerotized cuticle [referring to viam only] (Klann and Alberti, 2010: 227, fig. 226E, G).

interdigital condyli: Two distinct, semicircular articulation sclerites (condyli), devoid of setae (asetose areas), situated prolaterally (prolateral interdigital condyle, or pic) and retrolaterally (retrolateral interdigital condyle, or ric) at base of fixed (dorsal) finger (pls. 1, 2); condyli connected to each other via ventral manus plagula (vmp) (fig. 2A); together forming bicondylar hinge through which fixed finger articulates with movable (ventral) finger. Historical Use: *condyles* (Sørensen, 1914); *Condylus des Endringes* (Roewer, 1934: 54); external articulation sclerites (Muma, 1985: 2); two articulation points (Van der Meijden, 2012).

interdigital foramen: Circular opening on paturon where movable (ventral) finger attaches to manus through interdigital articular membrane and articulates with manus through interdigital condyli (fig. 2A).

interdigital sockets: Prolateral and retrolateral sockets on movable (ventral) finger into which pro- and retrolateral interdigital condyli rotate (pl. 2A, stippled line). Historical Use: *Gelenkpfannen* [joint sockets] (Roewer, 1934: 54, fig. 49).

macrosetae: Darker, more sclerotized, socketed setae that may be spiniform (rigid) or setiform (flexible). Historical Use: spiniform setae: *Dornen* (Kraepelin, 1901: 8; Roewer, 1934: 121); spines (translation from German by Turk, 1960; used by Lawrence, 1956; Maury, 1985; Gromov, 2003b; Reddick et al., 2010; Cushing and Castro, 2012); spinelike setae (Muma, 1976; Wharton, 1981); denticulate or spiculate, referring to "very short spinelike setae" (Wharton, 1981: 9); spiniform (Botero-Trujillo, 2014).

manus: Broad, largely setose, basal section of paturon (pl. 1A); usage consistent with that in some arthropods (e.g., crustaceans). Transition from manus to fixed (dorsal) finger historically vague and arbitrarily defined. Roewer (1934: 152, fig. 154) indicated position of bulbous base in Solpugidae as approximately where finger meets manus, dorsal to fondal teeth. Based on division of galeodid finger into *Endteil* and *Basalteil*, Birula (1937a) evidently regarded point between fixed finger proximal (FP) and medial (FM) teeth as start of finger. Wharton (1981: 42) considered fixed finger to start at distal end of fondal teeth. In present study, both fondal and median series teeth considered part of fixed finger, whereas interdigital condyli regarded as transition between manus and fixed finger (pl. 1A). Retrolateral interdigital condyle (ric), a well-defined landmark indicating start of fixed finger, identified for objective and repeatable comparisons of finger length. Historical Use: bases of falces (Putnam, 1883: 255); *Stamm der Mandibeln* [base of chelicera] (Kraepelin, 1901); *Hand* (Roewer, 1934: 53); *verdickten Teil beider Mandibeln* (Birula, 1937a: 568); *mano* (Mello-Leitão, 1938); trunk (Fichter, 1940); *main* (Panouse, 1960b); basal segment (Van der Meijden et al., 2012); manus (Botero-Trujillo, 2014).

medial notch (MN): Large toothless space on fixed (dorsal) finger, between fixed finger medial (FM) tooth and single fixed finger submedial (FSM) tooth situated close to fixed finger proximal (FP) tooth (fig. 7C, D); notch not considered homologous to fondal notch of Eremobatidae because medial notch situated distal to fixed finger proximal (FP) tooth, i.e., within median series of teeth, and fondal notch situated proximal to FP tooth; most prominent in Solpugidae (fig. 7C, pl. 109); diagnostic character for *Solpugema* Roewer, 1933 (Roewer, 1934: 420); similarly positioned, but less pronounced toothless spaces in other Solpugidae, e.g., see use of *Zahnlücke* by Kraepelin (1901: 59) to describe small toothless spaces such as in *Solpugista hastata* (Kraepelin, 1899); also present in Ammotrechidae (fig. 7D), e.g., in *Antillotrecha disjunctodens* Armas and Teruel, 2005, *Branchia angustus* Muma, 1951, *Branchia brevis* Muma, 1951, and apparently Karschiidae, e.g., in *Eusimonia mirabilis* Roewer, 1932 (Roewer, 1934: 143, fig. 141C; Muma, 1951: 136, figs. 305, 306, 311; Armas and Teruel, 2005: 161, fig. 9C; Armas, 2010: 522, fig. 1F). Historical Use: Ammotrechidae: *el diastema entre los dientes anteriores y el intermedio* (Armas, 2010: 522, fig. 1F). Solpugidae: *Zahnlücke* (Kraepelin, 1901, 1908a); *weiten, zahnlosen Lücke* (Roewer, 1934: 420).

median series teeth: All teeth on chelicera except fondal teeth on fixed (dorsal) finger; median series of fixed and movable (ventral) fingers, respectively (pl. 1A); previously referred only to teeth on fixed finger, but also applied here to teeth on movable finger. Historical Use: *canines plus incisives* (Dufour, 1861); outer/external series/row, including fondal teeth (Pocock, 1895; Birula, 1916; Lawrence, 1972); distal series (Purcell, 1899: 404); single series (Purcell, 1899, 1902; Hewitt, 1914a: 155); fang series (Lawrence, 1928: 262); dental series (Lawrence, 1935); median series (Wharton, 1981).

medioventral excrescence (MVE): Excrescence (convex enlargement) on ventral surface of fixed (dorsal) finger in male Melanoblossiinae (pls. 156B, 157C, 158C, E, 159); accommodates male flagellar complex and associated flagellar complex depression; depending on species, may be slightly (pl. 158C) or markedly (pl. 156B) developed.

medioventral organ (mvo): Round to oval depression(s) situated medioventrally on stridulatory plate (pls. 1C, 6B–D).

microsetae: Pale or transparent, weakly sclerotized socketed setae; uncommon or absent on chelicera.

movable finger fondal (*mff*) setae: Short series of plumose setae overlapping onto fond when chelicerae closed; arise on proximal margin of movable (ventral) finger (pls. 2B, 12A, 13A), and more dense on prolateral surface.

movable finger medial (MM) tooth: First primary tooth distal to proximal tooth, i.e., distalmost primary tooth, on movable (ventral) finger (pls. 21, 22A–D; table 6); putative serial homolog of fixed finger medial (FM) tooth, based on relative positions of FM and MM teeth when fingers closed (pl. 29). Historical Use: *Vorderzähn* (Kraepelin, 1899, 1901; Roewer, 1934: 53; Kraus, 1966); anterior tooth on movable finger (Lawrence, 1968); foretooth (El-Hennawy, 1998); anterior tooth, as *Ma* (Botero-Trujillo, 2014).

movable finger prodorsal (*mpd*) setae: Series of prolateral setae lining dorsal margin of setose area on movable (ventral) finger, directly ventral to asetose area (figs. 12, 13, pls. 12A, 13A, 14A, 15); setae plumose or acuminate, usually directed distodorsally at base.

movable finger prolateral carina (MPLC): Weakly to markedly developed longitudinal carina extending proximally from MPL tooth (pls. 57B, 58B, 73D); part of movable (ventral) finger prolateral series of teeth (pl. 1C; table 6); distinction between tooth and pronounced carina is continuum, representing states of single character.

movable finger prolateral series teeth: Series of prolateral teeth on movable (ventral) finger comprising movable finger prolateral tooth (MPL) and movable finger prolateral carina (MPLC) (pl. 1C; table 6).

movable finger prolateral setae: Prolateral setae on setose area of movable (ventral) finger (figs. 12, 13, pls. 12A, 13A, C, 14A, 15); comprises three series, i.e., movable finger prodorsal (*mpd*), promedial (*mpm*), and proventral (*mpv*) series. Historical Use: mesal setae of movable finger (Muma, 1951); median patch of bristles (Wharton, 1981: 51).

movable finger prolateral (MPL) tooth: Small to well-developed tooth situated prolaterally on movable (ventral) finger (pls. 1C, 15B, 22C), slightly proximal to movable finger proximal (MP) tooth; part of movable finger prolateral series of teeth (pl. 1C; table 6); in both sexes of Ammotrechidae (Roewer, 1934: 54; Muma 1951; Armas, 1994), most Eremobatidae (Muma, 1951), Rhagodidae (Roewer, 1934: 54; pl. 3C), and few species of Solpugidae (pls. 104A, C, 105A, C; Lawrence, 1954; 1961; Roewer, 1934: 429; Wharton, 1981). Historical Use: small tooth behind and on inner side of large tooth (Pocock, 1889: 474); *Nebenzahn* (Kraepelin, 1901); *medialen Wangenzahn* [medial cheek tooth of movable finger] (Roewer, 1934); mesal tooth (Muma, 1951); third tooth proximal to [rest of teeth on ventral finger] below level of anterior teeth (Lawrence, 1954, for *Ferrandia robusta*); supernumerary tooth (Brookhart, 1965) [not to be confused with mesal tooth, referring to movable finger medial (MM) tooth in description of *Hemerotrecha fruitana* Muma, 1951]; median tooth (Wharton, 1981); *diente basal interno* (*BI*) [of movable finger] (Maury, 1982: 126; 1984).

movable finger promedial (*mpm*) setae: Series of prolateral setae situated between movable finger prodorsal (*mpd*) and movable finger proventral (*mpv*) setae on setose area of movable finger (figs. 12, 13, pls. 12A, 13A, 14A, 15); setae acuminate, usually directed distally at base.

movable finger proventral (*mpv*) setae: Series of prolateral setae situated ventrally on setose area of movable (ventral) finger (figs. 12, 13, pls. 12A, 13A, 14A, 15); setae acuminate, sometimes more differentiated toward distal end of series (fig. 13), often directed ventrodistally at base.

movable finger proximal (MP) tooth: Proximalmost primary tooth on movable (ventral) finger (pls. 21, 22A–D; table 6); often largest tooth on movable finger; putative serial homolog of fixed finger proximal (FP) tooth. Historical Use: principal tooth (Pocock, 1889; Muma, 1951; Brookhart and Cushing, 2002); *Hauptzahn* [main tooth] (Kraepelin, 1899, 1901; Roewer, 1934: 53); chief tooth (Birula, 1926); *dent principale* (*DP*) [principal tooth] (Vachon, 1950; Panouse, 1956, 1960b); main tooth (Turk, 1960; Van der Meijden et al., 2012); main basal tooth (Wharton, 1981: 69); *principal* (*P*) (Maury, 1984); central tooth (El-Hennawy, 1998); primary tooth (Brookhart and Cushing, 2004; Catenazzi et al., 2009); posterior tooth (Bayram et al., 2011); principal tooth, as *Mp* (Botero-Trujillo, 2014).

movable finger retrolateral carina (MRLC): Blunt, angular longitudinal process on retrolateral surface of movable (ventral) finger into which rounded proximal margin of fixed finger closes (pls. 56B, 57B); in Dinorhaxinae, Rhagodidae (pl. 126F–H), and female, immature, and some adult male Hexisopodidae (pl. 56D, F, H).

movable finger submedial (MSM) tooth/teeth: One or more secondary teeth situated between movable finger proximal (MP) and movable finger medial (MM) teeth (pls. 21, 22A–D; table 6). Historical Use: intermediate teeth (e.g., Kraepelin, 1899, 1901; Roewer, 1934: 53; Panouse, 1960b: 176, fig. 2; Maury, 1982, 1984; Martins et al., 2004); intermediate teeth, as Mi_1, Mi_2 (Botero-Trujillo, 2014).

movable finger subproximal (MSP) teeth: Secondary teeth situated proximal to movable finger proximal (MP) tooth (pl. 22D; table 6).

movable finger subterminal (MST) teeth: Secondary teeth situated on movable finger mucron, i.e., between movable finger medial (MM) and movable finger terminal (MT) teeth (pl. 22D; table 6).

movable finger terminal (MT) tooth: Tip of movable (ventral) finger, i.e., distalmost part of mucron (pls. 21, 22A–D; table 6); putative serial homolog of fixed finger terminal (FT) tooth. Historical Use: apex [of finger]; terminal fang (Pocock, 1895; Purcell, 1899: 285); tip (Van der Meijden et al., 2012: 3412, fig. 1).

movable (ventral) finger: Second (ventral) segment of chelicera; articulates with first (basal) cheliceral segment (paturon), opposing fixed (dorsal) finger (pl. 1A). Historical Use: See table 5.

mucron: Distal, usually toothless section of finger (pls. 1A, 22D); portion of fixed (dorsal) and movable (ventral) fingers distal to fixed finger distal (FD) and movable finger medial (MM) teeth respectively, as measured from notch directly distal to FD or MM teeth respectively, to terminal tooth (FT or MT teeth respectively); also see fang. When FD and/or MM teeth absent, approximate position where FD or MM teeth would be located, inferred from its position in related taxa (see section on Dentition). However, proximal margin of mucron is often neither identifiable, nor deducible, rendering comparison among well delimited mucra impossible. Historical Use: terminal fang (Pocock, 1895: 84, 1899: 384; Purcell, 1899, 1902; Hewitt, 1919b: 30; Lamoral, 1972); toothless terminal portion of the dorsal jaw (Lawrence, 1927: 67); *Endteil*, *unbezahntes Ende des Fingers* (Birula, 1937a, measured from anterior end of median series to tip of finger) (see fixed finger for *Endteil* vs. *Basalteil*); *mucrón* (in Spanish literature, e.g., Maury, 1970; Rocha, 2002); untoothed finger (Hrušková-Martišová et al., 2010a); mucron (in English literature, e.g., González Reyes and Corronca, 2013). References to fang, mucron, and apex of finger are commonly used but not explicitly defined, especially not in a manner facilitating comparison among homologous structures across taxa. Rocha (2002: 446) defined mucron as the "distal portion of cheliceral fingers where there are no teeth." Applying this definition to a fixed finger with additional toothlike flanges and denticles anterior to the FD and MM teeth, on one hand, or to a fixed finger lacking all or most of the primary teeth, on the other, results in the term referring to structures unlikely to be homologous in different taxa, e.g., the use of terminal fang by Purcell (1899: 394) to describe the finger distal to the fondal teeth in an eremobatid chelicera (Purcell, 1899: 389, fig. 2). It is less ambiguous to define the mucron of the fixed and movable fingers based on position relative to the FD and MM teeth, respectively, but at the expense of being difficult or impossible to identify its proximal border when these teeth are absent.

mucron organ (mo): Small, round structure, paler than surrounding cuticle, situated prolaterally on mucron, slightly distal to fixed finger distal (FD) tooth; observed in both sexes of Galeodidae (pl. 60A) and Solpugidae (fig. 24B, pl. 27D, E), and in females and juveniles of Ammotrechidae and Mummuciidae (R. Botero-Trujillo, personal commun.); difficult to detect and may be present across the order; often situated on small prodistally directed toothlike structure; in male Solpugidae, often combined with distally directed, toothlike flagellar groove process (FGP) (fig. 24B, inset); function unknown. Historical Use: Reference to "tooth" in Solpugidae, but no reference to organ in any taxon: inner tooth on termimal fang (Purcell, 1899); *Zahnhöcker*, absent in *Solpugema erythronota* (Kraepelin, 1900) (vide Kraepelin, 1900: 6).

multidentate: Dental pattern in which all teeth approximately equal in size, regularly spaced, and situated in relatively straight row on fixed (dorsal) and/or movable (ventral) fingers, in lateral view (pl. 24R, fixed finger); differentiation between median row of teeth and retrofondal teeth often obscured; additional secondary teeth, mostly similar in size, often present proximal (MSP) and distal (FST and MST) to primary teeth in some Karschiidae, e.g., *Barrussus pentheri* (Werner, 1905) (pl. 52C, D), and Melanoblossiinae, e.g., *Lawrencega minuta* Wharton, 1981, and *L. procera* Wharton, 1981 (pl. 158B, F); subproximal and subterminal secondary teeth may be slightly raised relative to preceding teeth in Melanoblossiinae, e.g., *L. solaris* Wharton, 1981 (Wharton, 1981: 53, fig. 55), and usually readily identified due to comparatively smaller size, forming denticlelike, serrated gnathal edge; some taxa only exhibit tendency toward multidentate condition, i.e., some multidentate characters present, e.g., the eremobatid, *Horribates bantai* Muma, 1989 (pl. 78C, D). Historical Use: *Eusimonia*: *vielzähnig mit eineinzelnen grösseren Zähnen* (Kraepelin, 1901: 140).

paturon: First segment of solifuge chelicera, i.e., manus and fixed (dorsal) finger (pl. 1A). HISTORICAL USE: penultimate segment (Pocock, 1893); upper jaw (Purcell, 1899; Hewitt, 1919b: 33); *l'article basilaire* (Sørensen, 1914); basal segment of chelicera (Muma, 1951); fixed ramus (Dunlop, 2000); principal segment of chelicera (Klann and Alberti, 2010).

peduncle: Stem section of spoon-shaped flagellum in Galeodidae (pls. 30G, H, 31E); not considered homologous to stalk of composite flagellum (table 16). HISTORICAL USE: stem (Pocock, 1900b); *stiel* [stem] (Kraepelin, 1901; Birula, 1905; Roewer, 1934: 508); *Stiel des Flagellums* (Birula, 1905: 397); stalk (Hirst, 1912); stalk or peduncle (Birula, 1916); *Füßchen* or *Füsschen* [foot] (Birula, 1929b: 276, fig. 2; 1937a); stalk (Lawrence, 1956: 129; Turk, 1960).

plumose setae: Feathered setae with distinct shaft, finely branched distally (fig. 10B; Lawrence, 1956); restricted to prolateral cheliceral surface and lateral lips of rostrum in Solifugae, except for dorsalmost seta of retrolateral proximal setal cluster (*rlpc*) that may be weakly plumose. HISTORICAL USE: *gewimperte Borste* (Birula, 1913: 352, fig. 3); *gefiederte Wangenborstenreihe* (Birula, 1913); plumose setae (Wharton, 1981). Broadly applied by other authors, e.g., "plumose bristles" reported to protect stigmata of Karschiidae (Muma, 1976: 2), and palpal papillae described as "well feathered" (Hewit, 1919b: 12).

primary flagellum: Distinctly modified and well-differentiated ventral flagellar seta (*vfs*) in males (pls. 30–35, 36G, I, 38, 39A–F); also see flagellum or male flagellum. In Karschiidae (*Barrus*, *Barrussus*, and *Eusimonia*), usually dorsally curved, more or less cylindrical structure (pls. 30D, 31B). In Rhagodidae, ventral structure in diploflagellum (pls. 30F, 31D). HISTORICAL USE: *Barrus*, *Barrussus*, and *Eusimonia* (Karschiidae): flagellum (Simon, 1879: 128, 129, 131; Kraepelin, 1901: 140; Hirst, 1908, 1910); *Viertelkreishorn* or *Horn* (Roewer, 1934; Pieper, 1977); *Haken* (Birula, 1935a). Rhagodidae: flagellum (referring to both structures in diploflagellar complex, e.g., Kraepelin, 1901: 30; Roewer: 1934, 264).

primary teeth: Generally most differentiated (largest, often more sclerotized) teeth on cheliceral fingers (pls. 21, 22A–D, tables 6, 7 ; Pocock, 1895); three teeth on fixed (dorsal) finger (FP, FM and FD teeth), two on movable (ventral) finger (MP and MM teeth) in unmodified condition (pl. 22B). HISTORICAL USE: *canines* (Dufour, 1861); *dents principals* (Simon, 1879); chief denticles (Birula, 1926); large teeth (e.g., Turk, 1948; Wharton, 1981); main teeth (e.g., Lawrence, 1965b, 1968).

principal retrolateral finger (*principal rlf*) setae: Modified dorsal retrolateral finger (*rlf*) setae (fig. 14, pls. 16A, 144, 145); most distinct in daesiid genus, *Blossia* (Daesiidae); one, two, or three long, curved, tapering, nonplumose setae situated on retrodorsal surface of chelicera, slightly ventral to its dorsal margin, dorsal and distal to flagellum, directed distally and approximately parallel to fixed finger; here considered to also include modified *rlf* setae in other taxa, e.g., two distinctly elongated setae in Galeodidae (pl. 16A; Lawrence, 1954: 118). HISTORICAL USE: *Blossia*: Generally referring only to dorsalmost modified seta even in presence of a second, more ventral modified seta: differentiated distal bristle (Purcell, 1903a); distal dorsal bristle (Hewitt, 1914a: 158, 1919a; Lawrence, 1928); *spiculierter Borste* [spiculed bristle] (Roewer, 1934: 152); spiculated bristle (Lawrence, 1935); enlarged bristle on dorsal jaw (Lawrence, 1955); *Seta principalis* (Roewer, 1941); principal seta (Lawrence, 1965a; Lamoral, 1972; Wharton, 1981; Reddick et al., 2010). Lawrence (1935: 75) recognized similarity between a slightly modified, more ventrally situated *rlf* seta and two dorsal "spiculated setae," but did not regard these as possible serial homologs (also see Lawrence, 1935: 80, fig. 7); nor was a distinction recognized between "spiculated setae" situated retrolaterally on the chelicera, as part of the *rlf* setae, and "spiculated setae" situated prolaterally on the chelicera, as possible modified prolateral setae (e.g., Lawrence, 1935: 75, 76, 80, figs. 3, 4). Note: "principal setae" has also been used to refer to the flagella of Melanoblossiinae (*Seta principalis des Flagellum-Komplexes* sensu Roewer, 1941) and the karschiid, *Karschia*

(*Seta principalis flagella* sensu Roewer, 1934: 291), the spiniform setae of the flagellar complex (*fcs*) of Gylippinae (Wharton, 1981), and the retrolateral manus spiniform (*rlms*) seta of Gylippinae (*Spina principalis* sensu Roewer, 1934: 308; principle [sic] spine of Koç, 2011: 120, fig. 3).

prodorsal granular tooth: Granular structure parallel to medial (MM) tooth situated prodorsally on movable (ventral) finger of *Hexisopus* Karsch, 1879 (Hexisopodidae) (pls. 127A, C, E, 128A). HISTORICAL USE: mesal ridge or row of denticles (Wharton, 1981: 48); well-rounded tubercle (Wharton, 1981: 5); small but distinct tooth dorsomedially at distal edge of median patch of bristles (Wharton, 1981: 51).

prodorsal distal margin (pddm): Dorsal margin of asetose area of fixed (dorsal) finger situated directly dorsal to prodorsal distal (*pdd*) row of setae (pl. 1C); also see proventral distal margin (pvdm).

prodorsal distal (*pdd*) setae: Dorsal row of distal setae, situated directly ventral to prodorsal distal margin (pddm) of asetose area on fixed (dorsal) finger (pls. 12A, 13); *pdd* and *pvd* series connect distally at an angle; distalmost seta of *pdd* series (i.e., dorsal flagellar seta, or *dfs*) directly adjacent to distalmost seta of *pvd* series (i.e., ventral flagellar seta, or *vfs*); flagella and associated modified setae in flagellar complex hypothesized to be derived from *pdd* series (including *dfs*, i.e., precursor to secondary flagellum) and *pvd* series (including *vfs*, i.e., precursor to primary flagellum); modified flagellar complex subspiniform to spiniform (*fcs*) setae (pls. 30B–E, G, H, 31A–C, E, F, 32B, H, 33C, I) hypothesized to be derived from *pdd* setae.

prodorsal proximal (*pdp*) setae: One row and, in some taxa, a second, less developed row of *secondary pdp* setae on manus, extending longitudinally along prodorsal surface of chelicera (fig. 11, pls. 12A, 13, 14), often with prominent, elevated sockets in Eremobatidae and Gylippinae (e.g., pls. 72A, 85A, C, E). HISTORICAL USE: *Langsreihe von Borsten* (*lr*, Birula, 1913: 331, fig. 9; *l*, Birula, 1938: 81, fig. 52).

prodorsal serrate carina: Short ridge distal to median series of teeth on movable (ventral) finger, offset prolaterally from gnathal edge, in Hexisopodidae (*Chelypus*) (pl. 130F). HISTORICAL USE: row of minute inner teeth (Purcell, 1902: 225); serrated keels, inner row of...teeth confined to the distal end of the fang, row of minute teeth forming serrated ridge (Lamoral, 1973: 90); distally placed mesal ridge or row of denticles (Wharton, 1981: 45).

prodorsal spiniform setal cluster (*pdsc*): Small field of short spiniform setae prodistally on fixed (dorsal) finger next to callus in some *Chelypus* Purcell, 1902 (Hexisopodidae) (pls. 32C, 33E).

profondal (PF) teeth: Profondal row of fondal series (pls. 21A, 22C, E; table 6); profondal proximal (PFP) and profondal medial (PFM) teeth usually largest fondal teeth, typically tall and narrow, separated by either a diastema (e.g., Maury, 1976) or small profondal submedial (PFSM) tooth; two PFSM teeth rare, may be abnormal; single, rarely two, profondal subproximal (PFSP) tooth/teeth may be situated proximal to PFP tooth. HISTORICAL USE: *mediale* (*innere*) *Wangenzähne* (Kraepelin, 1901); *jugales internes* (Vachon, 1950); mesal row (Muma, 1951); *basal interno* (*BI*) (Maury, 1984); mesal fondal teeth (Fmf_{1-3}) (Botero-Trujillo, 2014).

profondal medial (PFM) tooth: See profondal teeth.

profondal proximal (PFP) tooth: See profondal teeth.

profondal submedial (PFSM) tooth: See profondal teeth.

profondal subproximal (PFSP) tooth/teeth: See profondal teeth.

prolateral dental process (PLDP): Prominent, carinate process on prolateral side of broad gnathal edge of cheliceral finger, at flagellar base in Hexisopodidae (pls. 2A, 130A, D, 131); in some species, prevents movement of flagellum past a certain point of rotation; hypothesized to be fused with primary teeth in *Hexisopus*. HISTORICAL USE: *Chelypus*: tubercle immediately adjacent to basal enlargement of flagellum (Hewitt, 1919c: 214). *Hexisopus*: slight proximal protuberance...bearing three small round teeth

(Lamoral, 1972: 120); one tooth near base of flagellum (Wharton, 1981: 52); low ridge adjacent to base of flagellum (Wharton, 1981: 51).

prolateral edge carinae: Distal longitudinal carinae situated on proventral surface of fixed (dorsal) finger and prodorsal surface of movable (ventral) finger; converge with gnathal edge and retrolateral edge carinae toward apex of cheliceral fingers (fig. 6C); also see gnathal edge carinae and retrolateral edge carinae.

prolateral interdigital condyle (pic): Semicircular articulation sclerite (condyle) situated prolaterally at base of fixed (dorsal) finger (fig. 2, pls. 1, 2); also see interdigital condyli and retrolateral interdigital condyle (ric).

prolateral setae: Setae on prolateral side of paturon (pls. 12A, 13, 14); comprises different series and setal fields, i.e., proventral distal (*pvd*) series, proventral subdistal (*pvsd*) series, prodorsal distal (*pdd*) series, prodorsal proximal (*pdp*) series, promedial proximal setal cluster (*pmpc*), promedial (*pm*) setal field, and provental (*pv*) series.

prolateral sockets: See interdigital sockets.

promedial proximal setal cluster (*pmpc*): Dense cluster of short, fine, hairlike setae at base of paturon directly dorsoproximal to stridulatory plate (fig. 11C, D, pls. 12A, 14B).

promedial (*pm*) setal field: Field of setae between stridulatory plate and proventral subdistal (*pvsd*) setal comb (pls. 12A, 13, 14); contains regularly spaced stridulatory setae (pls. 10, 11), when present, interspersed with less developed setae. Historical Use: *Querreihe* [transverse row] (*qr*, Birula, 1913: 331, fig. 9); *Das Mittelfeld der Innerseite der Mandibeln* (Birula, 1929a).

proventral distal (*pvd*) setae: One to three approximately regular rows of usually plumose setae lining ventral margin of fixed (dorsal) finger, from base to apex thereof (pls. 12A, 13, 14); distalmost seta in series (ventral flagellar seta, or *vfs*) hypothesized to be homologous to flagellum. Historical Use: *gefiederte Wangenborstenreihe* [row of plumose cheek bristles] (Birula 1913: 331, fig. 9); *soies ramifiées* [plumose setae] (Sørensen, 1914: 177); feathered bristles (Hewitt, 1919b); dental row (Lawrence, 1960); feathered bristles, plumose setae (e.g., Wharton, 1981). *Karschia* (Karschiidae): References to modified (highly elongated) *pvd* setae ventral to flagellum (pls. 1A, 46A, 47B): *säbelborsten* [saber bristles] (Kraepelin, 1901: 147); *grand soies ramifiées serrées* [large plumose setae] (Sørensen, 1914: 174); *spinae zygomaticae* (Roewer, 1934: 291).

proventral distal margin (pvdm): Ventral margin of asetose area of fixed (dorsal) finger directly ventral to proventral distal (*pvd*) row of setae (pl. 1C); also see prodorsal distal margin (pddm).

proventral (*pv*) setae: Narrow, longitudinal field of setae, usually sparsely arranged, along proventral surface of chelicerae, ventral to stridulatory plate (pls. 12A, 14A).

proventral subdistal (*pvsd*) setae: Series of nonplumose, acuminate setae situated proximal and parallel to proventral distal (*pvd*) setae (pls. 12A, 13, 14); includes comb at base of series. Historical Use: thickened smooth setae parallel to dental row (Lawrence, 1960).

proventral subdistal (*pvsd*) setal comb: Markedly differentiated, straight, apically pointed, rigid, and regularly spaced setae (pls. 12A, 13, 14); part of proventral subdistal (*pvsd*) row of setae, situated proximally in *pvsd* row.

retrodorsal process (RDP): Retrodorsal process at base of fixed (dorsal) finger in Eremobatidae, specifically *palpisetulosus* group of *Eremobates* (Muma, 1951) (fig. 7B); varies from shallow peaked ridge (pls. 68D, 69D) to pronounced, flangelike process (pls. 68J, 69F). Historical Use: ectodorsal process (Muma, 1951); dorsal process (Muma and Brookhart, 1988).

retrofondal (RF) teeth: Retrofondal row of fondal series teeth (pls. 21B, 22E, F; table 6); includes retrofondal apical (RFA) tooth/teeth (pls. 21B, 22F), i.e., one or more teeth in retrofondal row situated proximal to fixed finger primary (FP) tooth and distal to retrofondal medial (RFM) and retrofondal proximal (RFP) teeth, the two most-differentiated teeth of the retrofondal row (pls. 21B, 22E, F). RFP tooth situated proximal or subproximal in retrofondal row; usually equilateral triangle and largest tooth in retrofondal row. RFM tooth often similar in size and shape to RFP; intermediate to RFA and RFP teeth, but often distalmost tooth in retrofondal row. Retrofondal submedial (RFSM) tooth/teeth may be present between RFM and RFP teeth, and retrofondal subproximal (RFSP) tooth/teeth may be present proximal to RFP tooth; RFSM and RFSP teeth usually smaller than RFP and RFM teeth. Individual retrofondal teeth often more difficult to indentify than profondal teeth. Homology of teeth distal to RFM tooth and proximal to fixed finger proximal (FP) tooth, e.g., in Rhagodidae, and of denticles in fondal notch in Eremobatidae, remain unclear; pending further data, referred to as RFA teeth. Historical Use: *laterale* (*aussere*) *Wangenzähne* (Kraepelin, 1901); *jugales latérales* (Vachon, 1950); ectal row (Muma, 1951); *basal externo* (*BE*) (Maury, 1984).

retrofondal apical (RFA) tooth/teeth: See retrofondal (RF) teeth.

retrofondal medial (RFM) tooth: See retrofondal (RF) teeth.

retrofondal proximal (RFP) tooth: See retrofondal (RF) teeth)

retrofondal submedial (RFSM) tooth/teeth: See retrofondal (RF) teeth.

retrofondal subproximal (RFSP) tooth/teeth: See retrofondal (RF) teeth.

retrolateral convexity: Retrolateral curved elevation of fixed (dorsal) finger cuticle adjacent to bulbous base of flagellum; in Solpugidae (fig. 25A, visible through transparent base, pl. 48B, E, H).

retrolateral edge carinae: Distal longitudinal carina situated on retroventral surface of fixed (dorsal) finger and retrodorsal surface of movable (ventral) finger; converge with gnathal edge and prolateral edge carinae toward apex of cheliceral fingers (fig. 6C, pl. 5C); also see gnathal edge carinae and prolateral edge carinae.

retrolateral granular tubercle: Granular tubercle situated on retrolateral surface of movable (ventral) finger parallel to movable finger medial (MM) tooth, and approximately within row of granules extending along finger (pl. 13B, D).

retrolateral sockets: See interdigital sockets.

retrolateral finger (*rlf*) setae: Series of elongated, distally directed setae, often extending beyond tips of cheliceral fingers, situated close to margin of asetose area on fixed (dorsal) finger (fig. 14, pls. 12, 16) in all species and life stages of the order; also see principal retrolateral finger (*principal rlf*) setae. Historical Use: oblique row of simple bristles, bases of which are in a line more or less parallel with the dental series (Hewit, 1919b: 58: fig. 10); irregular row of simple bristles, more or less parallel to dental series (Lawrence, 1935: 75).

retrolateral interdigital condyl (ric): Semicircular articulation sclerite (condyle) situated retrolaterally at base of fixed (dorsal) finger (fig. 2, pls. 1, 2); also see interdigital condyli and prolateral interdigital condyle (pic).

retrolateral longitudinal carina: Longitudinal carina bearing granulation on retroventral surface of cheliceral movable (ventral) finger (fig. 8A); extending into retrolateral edge carina; approximately aligned basally with retrolateral proximal setal cluster (*rlpc*).

retrolateral manus (*rlm*) setae: Randomly situated setae on retrolateral to dorsal surface of cheliceral manus (pls. 12B, 16); homogeneous and less developed in females; various setiform and spiniform setae in males; spiniform setae typically increasing in length and robustness distally and, in dorsal view, usually arranged in row curving along proximal ("oblique row of 6–8 spinelike setae posteriorly" on chelicera, according to Wharton, 1981: 29) and retrolateral margins of chelicera (pl. 17). Historical Use: Gylippinae: *Nebendornen* (Birula, 1913: 332); *spina accessoriae* [accessory spines] (Roewer, 1934: 308); spiniform setae (Gromov, 1998).

retrolateral manus spiniform (*rlms*) seta: Robust, strongly spiniform seta, situated dorsomedially on retrolateral surface of manus in some male Gylippinae; distally directed (usually prolaterally, seldom retrolaterally), apically blunt or comblike, notched or spirally coiled (pls. 33I, 85B, 86B; Roewer, 1934: 120, fig. 101e, f); thickened seta in some females, in same position as homologous seta of males (pl. 85D, F; Birula, 1913: 324, fig. 1, plate VIII). Historical Use: *auffallend starkem Dornenpaar auf der dorsalen Fläche der Mdb*. (Kraepelin, 1901: 184); *Mandibulardorn* (Birula, 1907; *md* in Birula, 1913: 331, fig. 9); *Spina principales* [principal spines] (Roewer, 1934: 308); posterior main spine (as "true spines") (Lawrence, 1953); mandibular spine (Gromov, 1998); principle [sic] spine (Koç, 2011: 120, fig. 3).

retrolateral proximal setal cluster (*rlpc*): Clump of setae on small setose area situated proximally on retrolateral surface of movable (ventral) finger, at or near base of granular row extending along finger (pls. 12B, 18, 19); typically comprising cluster of setae aligned with granulation, and single seta situated dorsal to cluster. Historical Use: ectal cheliceral cluster (ECCS) setae (Muma, 1985); cheliceral setae (Punzo, 1998a: 228, figs. 7–13).

retrolateral setae: Setae on retrolateral surface of paturon and movable (ventral) finger (pls. 12B, 16); on paturon, may be divided into largely homogeneous, distally directed setae on finger (retrolateral finger setae, or *rlf*), and various setae on manus (retrolateral manus setae, or *rlm*); retrolateral proximal setal cluster (*rlpc*) on movable finger; no obvious difference in structure or position among setae situated dorsally to slightly prodorsally versus setae situated retrolaterally on chelicera, hence collectively grouped with respective retrolateral setae (pl. 17).

scapus: Broad, laminate section of spoon-shaped flagellum of Galeodidae (pls. 30G, 31E; Birula, 1916). Historical Use: blade (Pocock, 1900b; Hirst, 1912); *Plättchen* (Kraepelin, 1901); *Lanzette* (Birula, 1905; 1937a); *Löffel* [spoon] (Birula, 1929b: fig. 2); *Endlanzette* (Roewer, 1934: 508); expanded portion (Lawrence, 1956: 129); head (Turk, 1960: 114).

secondary flagellum: Modified dorsal flagellar seta (*dfs*) (pls. 30D, F, 31B, D), cf. primary flagellum; in Karschiidae (*Barrussus* and *Eusimonia*), usually fanlike membranous structure; in Rhagodidae, dorsal structure in diploflagellar complex. Historical Use: *Barrussus* and *Eusimonia* (Karschiidae): *Lamelle* (Simon, 1879: 131); *das Plättchen* (Kraepelin, 1901: 140; 1908a); vertical lamina (Hirst, 1908: 247); thin, hairy, wing-shaped plate (Hirst, 1910: 368); *Bläschenflagellum* (Roewer, 1934); *Flagellum* or *Flagellumplättchen* (Birula, 1935a); *Bläschen-Flagellum* (Pieper, 1977). Rhagodidae: flagellum, referring to both structures in diploflagellar complex (e.g., Kraepelin, 1901).

secondary prodorsal proximal setae (*secondary pdp*): Second, weaker row of setae, diverging from prominent prodorsal proximal (*pdp*) setae, sometimes present; structurally intermediate between promedial (*pm*) and *pdp* setae (e.g., pls. 10, 58B, 72A, 73A).

secondary teeth: Teeth smaller and less differentiated than primary teeth, situated proximal, intermediate, and distal to primary teeth (pls. 21B, 22; table 6). Historical Use: *incisives* [incisors] (Dufour, 1861); *Zwischenzähne* [intermediate teeth] (Kraepelin, 1899, 1901; Roewer, 1934: 53); minor teeth (Pocock, 1900b: 142, fig. 49; Hirst, 1908); intermediate teeth (Whittick, 1939; Muma, 1951; Turk, 1960; Lawrence, 1962a; El-Hennawy, 1998, Botero-Trujillo, 2014); *dent intermédiaire* (*DI*) [intermediate teeth] (Panouse, 1960b); *intermedio* (*I*) (Maury, 1984). Many authors (e.g., Kraepelin, 1901; Roewer, 1934; Maury, 1982; El-Hennawy, 1998; Rocha and Carvalho, 2006; Carvalho et al., 2010) restricted use of "intermediate teeth" to submedial teeth on fixed and movable fingers, and subsumed subdistal tooth under anterior teeth.

sessile flagellum: Flagellum without stalk, base and shaft (pls. 30, 31); in Dinorhaxinae, Galeodidae, Karschiidae, and Rhagodidae; structures resembling stalk, base and shaft can be identified in *Karschia* (Karschiidae) however, their homology with parts of composite flagellum is uncertain; nonrotatable, except in Galeodidae and *Karschia*, in which rotation more restricted than that of composite flagella; modification from original setal form does not involve longitudinal invagination; alembic canal absent.

setae: Multicellular, hollow, often slender processes produced by epidermal cells, situated movably in membranous sockets (Gorb, 2001; Gordh and Headrick, 2001), e.g., figure 10.

setiform flagellar complex (*sfc*): Type of flagellar complex comprising distinctly differentiated cluster of modified setae; all setae in complex, including flagellum, if present, setiform in appearance; *sfc* not to be equated with flagellum itself (i.e., single most differentiated seta derived from ventral flagellar seta, *vfs*); three types of *sfc* based on origin of modified setae, and arrangement and position on fixed (dorsal) finger (table 17), *type A* in Eremobatidae (pls. 37–39), *type B* in Lipophaginae (pl. 36A–F), and *type C* in Melanoblossiinae (pl. 36G–I); flagellum present in some Eremobatidae and Melanoblossiinae, absent in Lipophaginae; if present, flagellum weakly differentiated and/or obscured by other setae in cluster. Historical Use: Eremobatidae: flagellar complex (Muma, 1970a: 3; Brookhart and Cushing, 2004); flagellum composed of one or more modified setae (El-Hennawy, 1990: 26). Lipophaginae: flagellum not distinguishable (Purcell, 1903a); without flagellum (Hewitt, 1919b: 23); flagellum…consisting of modified plumose setae (Wharton, 1981: 39). Melanoblossiinae: *Flagellaren Borstengruppe* (Roewer, 1934: 139); *Flagellum-Komplex* (Roewer, 1941: 127); flagellum (Lawrence, 1972; Wharton, 1981; Gromov, 2003b).

setiform flagellar complex (*sfc*) dorsal series: Dorsal row or group of setae within setiform flagellar complex of Eremobatidae (pl. 38A, B); simple, tubular (e.g., *Eremobates*) to robust (e.g., *Hemerotrecha* Banks, 1903) setae, usually directed distally and/or curving dorsally; hypothesized to be homologous to prodorsal distal (*pdd*) setae.

setiform flagellar complex principal seta (*sfc principal seta*): Dorsalmost seta in type C setiform flagellar complex (*type C sfc*) of three melanoblossiine genera, *Lawrencega* Roewer, 1933, *Melanoblossia* Purcell, 1903, and *Unguiblossia* Roewer, 1941; most prominent seta in *sfc*, especially in *Melanoblossia*; may be as or more important functionally than flagellum in *sfc*. Historical Use: flagellum (Purcell, 1903); *seta principalis* (Roewer, 1941: 124); dorsalmost plumose seta (Wharton, 1981).

setiform flagellar complex, type A (*type A sfc*): Setiform flagellar complex in Eremobatidae comprising setae belonging to proventral distal (*pvd*) and prodorsal distal (*pdd*) series, and occasionally also proventral subdistal (*pvsd*) and/or promedial (*pm*) series (pls. 37–39; tables 15, 17); situated apically on prolateral surface of fixed (dorsal) finger, setae converging or arranged along it; never composed entirely of modified *pvd* setae as in *type B* and *type C sfc*; may be composed entirely of modified *pdd* setae (pl. 37D); extent of *sfc* always ill defined; flagellum, if present, setiform, may be associated with well-defined (e.g., in *Eremobates*) to weakly defined (e.g., in many *Eremochelis*) flagellar groove; cluster of setae may be heterogeneous (e.g., in *Eremobates*, pl. 38A) or relatively homogeneous (e.g., in *Eremorhax joshui*, pl. 37C) (table 15). In *Eremobates*, *Eremochelis* and, to a lesser extent *Eremothera*, comprising dorsal series (modified *pdd* setae), ventral series (*pvd* setae) and usually setiform flagellum. In other genera, e.g., *Chanbria*, *Eremocosta* Roewer, 1934, *Eremorhax*, and *Hemerotrecha* Banks, 1903, comprising similarly or differently modified setae originating from *pdd* setal series, with or without flagellum; setae may be striated but, if plumose, very weakly so.

setiform flagellar complex, type B (*type B sfc*): Setiform flagellar complex in Lipophaginae comprising one to two types of similarly modified, often plumose setae originating from proventral distal (*pvd*) series (pl. 36A–F; table 17); situated apically on prolateral side of fixed (dorsal) finger; modified setae clearly identifiable as part of *sfc*, usually distally directed, irrespective of shape of fixed finger; presumed absent in *Trichotoma michaelseni*.

setiform flagellar complex, type C (*type C sfc*): Setiform flagellar complex in Melanoblossiinae comprising modified proventral distal (*pvd*) setae arranged into unit with distinct, genus-specific shapes (pl. 36G–I; Wharton, 1981: 53, key); situated medially on proventral side of fixed (dorsal) finger in broad, shallow depression, the flagellar complex depression;

protected by convex ventral enlargement of the finger, the medioventral excrescence (MVE) (fig. 26, pl. 36G–I, table 17); setiform flagellum, if present, weakly differentiated, its presence in different melanoblossiine species needs to be verified; dorsalmost seta in complex, i.e., setiform flagellar complex principal seta (*sfc principal seta*) often more prominent than flagellum, if present.

setiform flagellar complex (*sfc*) ventral series: Ventral row or group of setae within setiform flagellar complex of Eremobatidae (pl. 38A, B); setae usually plumose, and bent apically to cover ventral part of flagellar groove; hypothesized to be homologous to proventral distal setae (*pvd*).

setiform flagellum: Flagellum that retains strong setiform character and affinities with plumose setae; in Eremobatidae (pls. 38, 39A–F) and Melanoblossiinae (seta "a" in pl. 36G, I); flagellum emerges and projects directly from chelicera without distinct flagellar stalk and base; unable to change direction and/or shape by hemolymph pressure.

socket margin elevation (sme): Low but distinct elevation on socket margin of flagellum; associated with flagellum of Galeodidae and *Karschia* (Karschiidae), primary flagellum of *Eusimonia* (Karschiidae), and secondary flagellum of Rhagodidae (pls. 30B, D, F, H, 31A, B, D, F, 40A, B, C).

spine: Stiff, sharp, pointed or tapered cuticular process without differentiation of cells, fixed immovably to body surface (Gorb, 2001; Gordh and Headrick, 2001); true spines rare in Solifugae, and on chelicera form hornlike (see dorsal hornlike process) or toothlike (see dorsal cheliceral spine) processes, e.g., in Karschiidae (pl. 30D, 31B) and some Daesiidae, and tubercles on callus of Hexisopodidae (fig. 6A, pls. 128D, E, 129, 130B).

stridulatory apparatus: Components putatively involved in stridulation, i.e., stridulatory plate, stridulatory ridges and stridulatory setae (pls. 1C, 8, 9, 10; Hansen, 1894: 185). Historical Use: *Stridulationsorgan*, *sr* [stridulatory organ] (Birula, 1913: 330); stridulatory organ (Hrušková-Martišová et al., 2008b: 443; Bayram et al., 2011).

stridulatory plate: Smooth, well-defined area, devoid of setae, at base of chelicera on prolateral surface; stridulatory ridges may or may not be present (fig. 24A, D, pls. 1C, 8–10). Historical Use: *plaque glabre de la face interne* (Dufour, 1861: 393); *Fläche* (Kraepelin, 1901); large, smooth area (Hewitt, 1913); stridulatory area (e.g., Hewitt, 1931); *Spiegelfläche* (Roewer, 1934: 52, fig. 47); stridulatory plate (Turk, 1960: 121).

stridulatory ridges: Approximately parallel, long, short, sometimes anastomosing ridges on stridulatory plate, aligned anteriorly with margin thereof (fig. 24A, D, pls. 1C, 8–10). Historical Use: sharp keels (Hansen, 1894); horny ridges (Pocock, 1898); stridulatory ridges (Pocock, 1900b: 133); *Stridulationsriefen* [stridulatory ridges] (Kraepelin, 1901; Birula, 1913); stridulatory ribs (Purcell, 1902); fine furrows (Hewitt, 1912); stridulatory lamellae (Lawrence, 1966: 7); stridulatory organ (or stridulatory ridges) (Wharton, 1981: 9); stridulatory apparatus [refers to stridulatory ridges only] (Botero-Trujillo, 2014).

stridulatory setae: Regularly arranged setae within promedial (*pm*) setal field (fig. 9, pls. 10, 11; Turk, 1960), distinctly modified in Eremobatidae, Galeodidae, and Rhagodidae; modification typically comprises swollen base inserted almost parallel to cheliceral surface and long, thin, acuminate tips (in Galeodidae and Rhagodidae), or thin seta inserted almost parallel to cheliceral surface on elevated socket (in Eremobatidae). Turk (1960) identified several types, i.e., galeodid type I (*arabs* type) (fig. 9A, pl. 11I), galeodid type II (*araneoides* type) (fig. 9B, pl.11G, H), galeodid type III (*medusae* type) (fig. 9C), to which may be added an eremobatid type (fig. 9E, pl. 11E) and, similar to, but more spiniform than galeodid type II form, a rhagodid type (fig. 9D, pls. 10, 11F). Historical Use: spiniform setae (Birula, 1925); stridulatory setae (Turk, 1960); *soies flagellées* (Benoit, 1964); spiny bristles (Dumortier, 1964); stridulatory hairs (Cloudsley-Thompson and Constantinou, 1984); stridulatory bristles (Hrušková-Martišová et al., 2008b).

subterminal flange (STF): Toothlike flange on gnathal edge of fixed (dorsal) finger between terminal (FT) tooth and distal (FD) tooth in Daesiidae (pls. 144B–F, arrows, 145B–F) and Solpugidae (pl. 109B, D–F, arrows). Historical Use: *Solpugema erythronota* (Kraepelin, 1900) (Solpugidae): *zahnartig vorspringendem Eck* (Kraepelin, 1901).

supernumerary teeth: Obsolete term in solifuge dentition; described various teeth/denticles (see section on Dentition) assigned to categories defined in the present contribution.

styletlike fixed finger: Apically tapering distal part of fixed (dorsal) finger; narrowing of finger between fondal series and fixed finger proximal (FP) tooth into stylet shape; dentition on stylet-shaped part usually absent, at most vestigial; common in male Eremobatidae (pl. 65B, F, H, J) and Gylippinae (pl. 85B).

ventral digital plagula (vdp): Asetose margin at base of movable (ventral) finger, flanking ventral interdigital articular membrane (viam) distally (pls. 1B, C, 2C, 6A).

ventral flagellar seta (v*fs*): Apicalmost seta of proventral distal (*pvd*) series; hypothesized precursor of primary male flagellum (pls. 12A, 13, 46C, 47).

ventral interdigital articular membrane (viam): See interdigital articular membrane (iam).

ventral manus plagula (vmp): Asetose, U-shaped area on manus lining interdigital foramen ventrally, and flanking ventral interdigital articular membrane proximally (pls. 1B, C, 2C, 6A); connects pro- and retrolateral condyli. Historical Use: *Chitinwulst* (Roewer, 1934: 55).

ventral notch (VN): Point where ventral side of movable (ventral) finger abruptly narrows toward apex, in Eremobatidae (fig. 7B; Muma and Brookhart, 1988).

ventrodistal concavity: Oval, ventral to retroventral concavity on asetose area of fixed (dorsal) finger of some male Eremobatidae, e.g., *Eremocosta titania* (pls. 37C, 73B), *Hemerotrecha banksi* Brookhart and Cushing, 2008 (Brookhart and Cushing, 2008: 50, fig. 3). Historical Use: groove (Muma, 1951); mesal ventral groove (Brookhart and Cushing, 2008: 50, fig. 3).

APPENDIX 2

Material Examined

Abbreviations for collections are as follows: American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CAS); Denver Museum of Nature and Science, Denver, Colorado (DMNS); Hebrew University of Jerusalem, Israel (HUJI); Kirikkale University, Turkey (KUT); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Musée Royal de l'Afrique Central, Tervuren, Belgium (MRAC); National Collection of Arachnida, Plant Protection Research Institute, Pretoria, South Africa (NCA); National Museum of Namibia, Windhoek, Namibia (NMNW); KwaZulu-Natal Museum, Pietermaritzburg, South Africa (NMSA); Senckenberg Museum, Frankfurt, Germany (SMF), including the Roewer collection (R); Tel Aviv University, Zoology Museum, Israel (TAUZM); Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa (TMSA); Zoological Museum, Lund University, Sweden (ZMLU); Zoologisches Museum der Universität Hamburg, Germany (ZMUH).

AMMOTRECHIDAE ROEWER, 1934

AMMOTRECHINAE ROEWER, 1934

Ammotrecha stollii (Pocock, 1895): **NICARAGUA: Chinandega Province:** El Viejo, Hacienda (Hostel) Cosiquina, 12°54′33.0″N 87°30′40.0″W, 18 m, 27.xi.2007, C. Viquez and J. Mata, 5♂ (AMNH [LP 8605]).

Pseudocleobis andinus (Pocock, 1899): **ARGENTINA: Mendoza Province:** Puente del Inca, 32°49.568′S 69°54.606′W, 2759 m, 2.

xi.2003, C.I. Mattoni, L. Prendini, and J.A. Ochoa, 2♂, 1♀, 2 juv. (AMNH [LP 2384]).

NOTHOPUGINAE MAURY, 1976

Nothopuga cuyana Maury, 1976: **ARGENTINA: Córdoba Province:** 20 km N of San José de las Salinas, E border of Salinas Grandes, 15.xi.2002, C.I. Mattoni, J.A. Ochoa, and M. Moyano, 1♂, 2 juv. (AMNH [LP 2263]).

OLTACOLINAE ROEWER, 1934

Oltacola gomezi Roewer, 1932: **ARGENTINA: Córdoba Province:** 20 km N of San José de las Salinas, E border of Salinas Grandes, 15.xi.2002, C.I. Mattoni, J.A. Ochoa, and M. Moyano, 2♂ (AMNH [LP 2262A, 10681]).

SARONOMINAE ROEWER, 1934

Procleobis patagonicus (Holmberg, 1876): **ARGENTINA: Neuquen Province:** Picun Leufu, 39°32′13.5″S 69°13′21.8″W, 399 m, 25.i.2005, M. Magnanelli and E.G. López, 1♂ (AMNH [LP 4235]).

INCERTAE SEDIS

Sedna pirata Muma, 1971: **CHILE: Region IV (Coquimbo):** *Choapa Province*: Caleta Totoralillo, 32°01.569′S 71°30.889′W, 5 m, 4.xi.2003, L. Prendini, C.I. Mattoni, and J.A. Ochoa, 1♀ (AMNH [LP 2362]).

CEROMIDAE ROEWER, 1933

Ceroma inerme Purcell, 1899: **NAMIBIA: Karas Region:** *Lüderitz District*: Diamond Area 1: Sperrgebiet National Park: Bogenfels, 27°27′27.6″S 15°23′28.6″E, 31.viii.2006, EduVentures 9 Expedition, 1♀ (AMNH [LP 8425]); S of Bogenfels Arch, 27°27′36.2″S 15°23′38.6″E, 9 m, 14–16.vi.2008, C. Kaapehi and B. Muramba, 8♂, 1♀ (NMNW 13632), 14–18.vi.2008, C. Kaapehi and B. Muramba, 2♂ (AMNH [LP 9864]).

Ceroma ornatum Karsch, 1885: **KENYA: Eastern Province:** Mount Kasigau, Jora Village, xii.2001, E. Selempo, 1♂ (MRAC 2013.106).

Ceroma swierstrae Lawrence, 1935: **SOUTH AFRICA: Western Cape Province:** *Bredasdorp District*: De Hoop Nature Reserve, 26.iii.2005, C. Haddad, 1♂ (NCA 2009/4355]).

Ceromella sp: **SOUTH AFRICA: Western Cape Province:** *Vredendal District*: Farm Perseel Weskus 197, 31°29.038′S 18°01.367′E, 16 m, 21–26.ix.2007, C. Lyons, J. Mingo, and R. Lyons, 1♂ (AMNH [LP 8527]).

DAESIIDAE KRAEPELIN, 1899

DAESIINAE KRAEPELIN, 1899

Biton (*Biton*) *browni* (Lawrence, 1963): **NAMIBIA: Karas Region:** *Keetmanshoop District*: Kokerboom Forest on Farm Gariganus 157, 14 km NE of Keetsmanshoop, 26°28.914′S 18°14.660′E, 1092 m, 25.i.2004, L. Prendini and E. Scott, 1♂, 1 juv. (AMNH [LP 3633]).

Biton (*Biton*) *rossicus* (Birula, 1905): **UZBEKISTAN: Surkhandarya Area:** *Angor District*: Kattakum Desert, 4.5 km NE of Uchkyzyl, 37°22.549′N, 67°16.618′E, 331 m, 19.v.2003, L. Prendini and A.V. Gromov, 1♂, 1♀ (AMNH [LP 3959]).

Biton (*Biton*) *zederbaueri* (Werner, 1905): **TURKEY: Kilis Province:** *Musabeyli District*: Hasançali Village, 36°53′30″S 36°47′35″E, 27.v.2006, E.A. Yağmur, 1♂ (KUT).

Biton (*Biton*) sp. 1: **NAMIBIA: Kunene Region:** *Opuwo District*: Baynes Mountains, Okaombo Valley, 17°02′44.7″S 13°03′51.9″E, 985 m, 18.iv.2006, EduVentures 8 Expedition, 10♂, 1♀ (NMNW 13278).

Biton (*Biton*) sp. 2: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Augrabies 109, Gaap River, viii.2005, EduVentures 7 Expedition, 1♂ (NMNW).

Biton (*Biton*) sp. 3: **NAMIBIA: Karas Region:** *Lüderitz district:* Farm Klein Aus 8, 26°39′06.9″S, 16°14′38.0″E, 1382 m, 31.x.2008, T. Greyling, 1♂ (AMNH [LP 9852]).

Biton (*Biton*) sp. 4: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Stamprivier 108, 27°28′06.8″S 17°52′29.8″E, 888 m, 6.xi–15.xii.2008, R and D.R. Brand, 1♂ (NMNW).

Biton (*Biton*) sp. 5: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Gocheganas 26, 20.xii–20.i.1982, M.L. Penrith, 1♂ (NMNW 12228).

Biton (*Biton*) sp. 6 (*namaqua* group): **NAMIBIA: Khomas Region:** *Windhoek District*: Auas Mountains, Farm Regenstein 32, 22°42′39.0″E 17°02′21.8″E, 2022 m, 16.ii–16.iv.2009, J.F. Kaudinge, B.K. Muramba, and T.L. Bird, 1♂ (NMNW).

Biton (*Biton*) sp. 7: **NAMIBIA: Khomas Region:** *Windhoek District*: Windhoek, Ludwigsdorf, 22°33′37.1″S 17°06′41.7″E, 1715 m, 16.vi.2009, J. Walter and U. Kirchner, 1♂ (AMNH [LP 9853]).

Biton (*Biton*) sp. 8: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Gocheganas 26, 22.iv–20.v.1982, M.L. Penrith, 3♂ (NMNW 12336).

Blossia grandicornis Lawrence, 1929: **SOUTH AFRICA: Northern Cape Province:** *Prieska District*: Farm Good Hope, ca. 30 km SW of Prieska, 29°49′11″S 22°31′42″E, 9–18.i.2006, M. Burger, D. Haarmeyer, and D. Massyn, 4♂, 1♀ (AMNH [LP 5905]).

Blossia sabulosa Lawrence, 1972: **NAMIBIA:** *Lüderitz District*: Diamond Area 1: Namib-Naukluft Park: Garub plains, 26°31′35.1″S 16°04′44.9″E, 910 m, 14.xii.2008–25.i.2009, T.L. Bird, L. Prendini, and J. Huff, 1♂ (NMNW).

Blossia spinicornis Lawrence, 1928: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Brakwater 48, 22°25′27.0″S 17°02′09.2″E, 1516 m, 20.ii–14.iv.2009, J.F. Kaudinge, B.K. Muramba, and T.L. Bird, 1♂ (NMNW).

Blossia tricolor Hewitt, 1914: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Stamprivier 108, 27°28′06.8″S 17°52′29.8″E, 888 m, 6.xi–15xii.2008, R. and D.R. Brand, 1♂ (NMNW).

Blossia cf. *purpurea* Wharton, 1981: **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Ganab, 4.5 km S, 23°08′37.4″S 15°31′17.3″E, 1045 m, 20.i.2009, T.L. Bird, J. Huff, and L. Prendini, 1♂ (NMNW 13893).

Blossia cf. *rooica*: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Stamprivier 108, 27°28′06.8″S 17°52′29.8″E, 888 m, 6.xi–15xii.2008, R. and D.R. Brand, 1♂ (NMNW).

Blossia sp.: **NAMIBIA: Karas Region:** *Lüderitz District*: Diamond Area 1: Namib-Naukluft Park: Garub plains, 26°31′35.1″S 16°04′44.9″E, 910 m, 14.xii.2008–20.i.2009, T.L. Bird, J. Huff, and L. Prendini, 1♂ (NMNW).

Gluviinae Roewer, 1933

Eberlanzia flava Roewer, 1941: **NAMIBIA: Erongo Region:** *Walvis Bay District*: Kuiseb Delta, 16.viii.1976, S. Louw, 9♂, 1♀, 1 juv (NMNW 11176).

Gluvia dorsalis (Latreille, 1817): **PORTUGAL: Évora:** Herdade da Mitra, 38°31.937′N 08°01.096′W, 12.vii.2006, S. Henriques, 1♂ (AMNH [LP 6093]).

Gluviopsinae Roewer, 1933

Gluviopsilla discolor (Kraepelin, 1899): **TURKEY: Hatay Province:** Gorentas, 35°54′50.9″N 36°09′29.2″E, 538 m, 31.v.2007, A.V. Gromov and H. Koç, 4♂, 2♀, 1 juv. (AMNH). **Kayseri Province:** *Melikgazi District*: Yenihayat Village, 37°42′25.4″N 44°00′34.1″E, 1535 m, 22.vi.2007, A.V. Gromov and H. Koç, 1♂ (AMNH [LP 7516]). **Kilis Province:** *Musabeyli District*: Hasançali, 2 km SW, 36°52′47.2″N 36°47′42.4″E, 755 m, 26–27.v.2007, A.V. Gromov, H. Koç and E.A. Yağmur, 3♂, 4♀, 1 juv. (AMNH). **Şanliurfa Province:** *Akçakale District*: Edebey, 36°50′40.7″N 38°40′57.8″E, 532 m, 31.v.2007, A.V. Gromov, H. Koç and E.A. Yağmur, 2♂, 3♀, 5 juv. (AMNH).

Gnosippinae Roewer, 1933

Gnosippus klunzingeri Karsch, 1880: **ISRAEL:** *Southern District*: Arava Valley, 30°43.645′N 35°12.091′E, 17.vi.2009, T. Hacket, 1♂ (HUJI 770).

Hemiblossia australis (Purcell, 1902): **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Holoog 106, 27°24′06.9″S 17°47′17.5″E, 793 m, 16.xii.2008, R. Brand, 1♂, 1 juv. (AMNH [LP 9866]).

Hemiblossia etosha Lawrence, 1927: **NAMIBIA: Otjozondjupa Region:** *Grootfontein District*: Farm Uisib 427, 19°32′54.1″S 17°14′06.8″E, 1343 m, 29.xii.2008–2.i.2009, T.L. and C. Bird, and K. Schoeman, 1♂ (AMNH [LP 9854]), 1♂, 1juv. NMNW 13798).

Hemiblossia oneili Purcell, 1902: **NAMIBIA: Karas Region:** *Karasburg District*: Gondwana Cañon Park: Farm Karios 8, 27°40′28.3″S 17°49′10.6″E, 896 m, 7.xi–12.xii.2008, R. and D.R. Brand, 1♂ (NMNW).

Hemiblossia sp. 1: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Holoogberg 107, Middelpos, 27°32′40.9″S 17°53′36.6″E, 965 m, 6.xi–13.xii.2008, R. and D.R. Brand, 1♂ (NMNW).

Hemiblossia sp. 2: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Stamprivier 108, 27°28′06.8″S 17°52′29.8″E, 888 m, 6.xi–15xii.2008, R. and D.R. Brand, 1♂ (NMNW).

NAMIBESIINAE WHARTON. 1981

Namibesia pallida Lawrence, 1962: **NAMIBIA: Erongo Region**: *Omaruru District*: Brandberg, base of Ga-Aseb Gorge, 21°13′41.6″S 14°34′44.1″E, 781 m, 21.xii.2003, L. Prendini, T.L. Bird, and N. Krone, 1♂ (AMNH [LP 10721]). **SOUTH AFRICA: Northern Cape Province:** *Namaqualand District*: Farm Goodhouse 23, 1 km W of turnoff to Goodhouse, on Pella–Concordia road, 28°58.684′S 18°13.337′E, 450 m, 2–3.iii.2005, L. Prendini and E. Scott, 1♀ (AMNH [LP 4017]).

INCERTAE SEDIS

Ammotrechelis goetschi Roewer, 1934: **CHILE: Region IV (Coquimbo):** *Choapa Province*: Quereo, 19.viii.2009, J. Pizarro, 2♂, 1♀ (AMNH [LP 10673]).

Ceratobiton styloceros (Kraepelin, 1899): **ISRAEL:** *Southern District*: Big Crater, 21.i.1962, 1♂ (HUJI 55).

EREMOBATIDAE KRAEPELIN, 1901

EREMOBATINAE KRAEPELIN, 1901

Eremobates actenidia Muma, 1989: **U.S.A.: Utah:** *Emery County*: 38.7256°N 110.4323°W, 1394 m, 8–9.vi.2013, P.E. Cushing, L. Petrie, R. Wicker, and J. Brainard, 6♂, 1♀ (DMNS ZA.33522).

Eremobates ajoanus Muma and Brookhart, 1988: **U.S.A.: Arizona:** *Pima County*: Ajo Road, S of Ajo, 32.67°N 112.86°W, 335 m, 4.vi.1975, C. Moss, paratype♀ (DMNS ZA.17311); Ajo, 10 mi. N, 32.34°N 112.85°W, 16.v.1972, C. Moss, paratype♂ (DMNS ZA.17384); 31.942726°N 112.811093°W, 8.vi.2013, 2♂ (DMNS ZA.33218, ZA.33222); 31.941989°N 112.811877°W, 9.vi.2013, 1♂ (DMNS ZA.33219).

Eremobates angustus Muma, 1951: **U.S.A.: Arizona:** *Cochise County*: Huachuca Mountains, Ramsey Canyon, 31.450081°N 110.305752°W, 1494 m, 10 vii.1941, paratype♂ (DMNS ZA.16789).

Eremobates ascopulatus Muma, 1951: **U.S.A.: Nevada:** *White Pine County*: Great Basin National Park, 39.01511°N 114.12556°W, 1631 m, 7–8.vi.2013, P.E. Cushing, 4♂, 1♀ (DMNS ZA.33524), 39.01511°N 114.12556°W, 1631 m, 9.vii.2013, P.E. Cushing and P. Gorring, 5♂ (DMNS ZA.33529).

Eremobates bajadae Muma and Brookhart, 1988: **U.S.A.: New Mexico:** 10 mi. W of Carlsbad, 1.5 mi. N on Dark Canyon Road after second cattle guard, 32°17.082′N 104°18.000′W, 7–10.vi.2004, J. Huff and R.C. West, 1♂ (AMNH [LP 5740]).

Eremobates bixleri Muma and Brookhart, 1988: **U.S.A.: Arizona**: *Pima County*: Tucson, 32.22167°N 110.92583°W, 20.iv.1968, 896 m, D.E. Bixler, paratype♂ (DMNS ZA.17386).

Eremobates chihuaensis Brookhart and Cushing, 2002: **MEXICO: Chihuahua:** *Chihuahua Municipality*: Chihuahua, 22 mi. S, 4400 ft, 25 viii.1980, J.B. Karren, holotype♂ (DMNS ZA.10002).

Eremobates corpink Brookhart and Cushing, 2004: **U.S.A.: Utah:** *Kane County*: Coral Pink sand dunes, 21.vii.1998, R.W. Baumann, holotype♂ (DMNS ZA.17380); Coral Pink sand dunes, Ponderosa Grove campground, 37°05′N

112°40′W, 11.vi.2002, S.M. Clark, paratype♀ (DMNS ZA.17379); Off Hwy 276, S of junction Hwy 95, 37.54738°N 110.04059°W, 1868 m, 28.v.2012, P.E. Cushing, L. Petrie, B. Trierweiler, and A. McMichael, 2♂, 3♀ (DMNS ZA.33748).

Eremobates gerbae Brookhart and Cushing, 2002: **U.S.A.: Arizona:** *Pima County*: Mack Burn Area, 32.13194°N 110.51889°W, 30.viii.1994, P. Gerba, holotype♂ (DMNS ZA.10000), 8.x.1995, P. Gerba, paratype♀ (DMNS ZA.10001), 29.iii.1995, P. Gerba, 1♂, 1♀ (DMNS ZA.16189).

Eremobates icenoglei Brookhart and Cushing, 2004: **U.S.A.: California:** *Riverside County*: Winchester, 33°42′N 117°05′W, 22.viii.1968, W. Icenogle, holotype♂ (DMNS ZA.17376), 29.viii.1996, W. Icenogle, paratype♀ (DMNS ZA.17377).

Eremobates inkopaensis Brookhart and Cushing, 2005: **U.S.A.: California:** *Imperial County*: Meyer Gorge, Ko Pah Valley, 32.68°N 116.06°W, 570 m, 27.iii.1982, J. Berrian, paratype♂ (DMNS ZA.17381), 32°43′N 116°02′W, 17.iv.1982, J. Berrian, paratype♀ (DMNS ZA.17310).

Eremobates kiseri Muma and Brookhart 1988: **U.S.A,: Texas**: Turkey, 6 mi. SE, 6.v.1970, D. Kiser, paratype♀ (DMNS ZA.17385), 1♀ (DMNS ZA.16791).

Eremobates norrisi Muma and Brookhart 1988: **U.S.A.: New Mexico:** *Hidalgo County*: Lordsburg, 32.345639°N 108.6957°W, 1306 m, 15.v.1975, M.H. Muma, paratype♀ (DMNS ZA.17383).

Eremobates pallipes (Say, 1823): **U.S.A.: New Mexico:** *Socorro County*: Sevilleta National Wildlife Refuge, Long Term Ecological Survey Station, 34.350°N 106.883°W, 1471 m, 31.vii.1991, J.O. Brookhart, 1♂ (DMNS ZA.16258). **Utah:** *San Juan County*: 4 mi. S of Blanding, State Rt 210 and Hwy 191, 10.vi–26.viii.2000, J.O. and I.P. Brookhart, 1♀ (DMNS ZA.15662).

Eremobates palpisetulosus Fichter, 1941: **U.S.A.: Colorado:** *Denver County*: Denver, 135 S Taylor Ave, 17.vii.2003, B. Tiemann, 1♂ (DMNS ZA.15683). *Fremont County*: Phantom Canyon Road, 4.5 mi. from Hwy 50, 38.512°N 105.112°W, 1829 m, 10.v–10.vii.1999, J.O. and I.P. Brookhart, 1♀ (DMNS ZA.15686).

Eremobates polhemusi Muma and Brookhart, 1984: **U.S.A.: Utah:** *San Juan County*: 4 mi. N of Bluff, Hwy 191 and UT 240, 10.vi–26.viii.2000, J.O. and I.P. Brookhart, 1♀ (DMNS ZA.10004).

Eremobates socal Brookhart and Cushing, 2004: **U.S.A.: California:** *San Bernardino County*: Joshua Tree National Park: 29 Palms, Park Headquarters, 34.128042°N 116.040437°W, 1070 m, 22.viii.1994, paratype♀ (DMNS ZA.17378).

Eremobates tuberculatus (Kraepelin, 1899): **U.S.A.: California:** *Calaveras County*: Mokelumne Hill, 1♂ (AMNH).

Eremobates cf. *palpisetulosus*: **U.S.A.:** 1♂ (AMNH).

Eremocosta gigasella (Muma, 1970): **U.S.A.: New Mexico:** *Socorro County*: Sevilleta Long Term Ecological Research Center, 34°21′10.8″N 106°52′55.2″W, 1478 m, 26.vii.1993, 1♀ (DMNS ZA.17350).

Eremocosta titania (Muma, 1951): **U.S.A.: California:** *Imperial County*: Ogilby Road, N of Hwy 8, 32°46.180′N 114°50.209′E, 74 m, D. Wood, 1♂ (DMNS ZA.16319). *Inyo County*: Death Valley National Park Saline Valley Dunes, just off Saline Valley Road, 36°45.188′N 117°51.795′W, 343 m, 4.ix.2005, L. Prendini and R. Mercurio, 1♂ (AMNH [LP 5035]). *San Bernardino County*: 29 Palms, 5 mi. NW Sunshine Peak, 34.700°N 116.479°W, 914 m, 17.v.2004, G. Pratt, C. Pierce, and Tilborg, 1♂ (DMNS ZA.16320).

Eremothera drachmani Muma, 1986: **U.S.A.: Arizona:** *Pima County*: Catalina State Park, campsite A and B, 32.42445°N 110.92271°W, 822 m, 28–29.vii.2011, P.E. Cushing, 1♂ (DMNS ZA.28156).

Eremothera sculpturata Muma, 1951: **U.S.A.: Arizona:** *Pima County*: 1.3 mi. S of State 86 on road to Pisinimo, 32.099°N 112.296°W, 624 m, 1.ix.1965, T. Briggs, 1♀ (DMNS ZA.16477). *Yavapai County*: Congress, 9 mi. W, 34.113°N 112.976°W, 914 m, 30.vii–24.viii.1998, R.S. Beal, 1♂ (DMNS ZA.16475); 6 mi. from Wickenburg, 13.viii.1976, V. Roth, 1♂ (DMNS ZA.16476).

Horribates bantai Muma, 1989: **U.S.A.: California:** *San Bernardino County*: Granite Cove, 5 mi. N

I-40 on Kelbaker Road, 34.78°N 115.65°W, 1341 m, 2.vii.1998, E. Fessler, 1♀ (DMNS ZA.17691).

Therobatinae Muma, 1951

Chanbria regalis Muma, 1951: **U.S.A.: California:** *Imperial County*: Algodones Dunes, at junction of Olgiby Road (S34) and Interstate Hwy 8, 32°45.454′N 114°50.203′W, 50 m, 31.viii.2005, R. Mercurio and L. Prendini, 1♂, 3♀ (AMNH [LP 10746]).

Eremochelis acrilobatus (Muma, 1962): **U.S.A.: Arizona:** *Coconino County*: Grand Canyon South Rim, vi.1954, M.A. Cazier, 1♂ (DMNS ZA.16067).

Eremochelis albaventralis Brookhart and Cushing, 2005: **MEXICO: Estado de Mexico:** *Juchitipec Municipality*: Juchitipec, 7 km (air) WSW, 19.085887°N 98.946848°W, 2734 m, 24.vii.1987, J. Doyen, paratype♂ (DMNS ZA.17382).

Eremochelis andreasana (Muma, 1962): **MEXICO: Baja California Sur:** *Mulegé Municipality*: San Ignacio, 27°18′04″N 112°53′11.1″W, 125 m, 17.vii.2004, O.F. Francke, W.E. Savary, E. González, and A. Valdez, 1♂ (AMNH [LP 3184]). **U.S.A.: California:** *Riverside County*: Andreas Canyon, 24.iv.1954, J.G. Rozen, holotype♂ (AMNH).

Eremochelis bilobatus (Muma, 1951): **U.S.A.: Colorado:** *Douglas County*: Roxborough State Park, Willow Creek Trail, 1.25 mi. S of Visitor Center, 39.420°N 105.065°W, 1926 m, 18.vi.1999, B. Nelson, 1♂ (DMNS ZA.16039).

Eremochelis insignatus Roewer, 1934: **U.S.A.: California:** *San Bernardino County*: Joshua Tree National Monument, 33.9476°N 116.1717°W, v.2000, USGS-San Diego, 1♂, 1♀ (DMNS ZA.16136). **California:** *Imperial County*: Hwy 78 at Junct. San Felipe Creek, 10.5 mi. W of Junct. Hwy 86, 33°07.538′N 116°02.660′W, 4.vi.2008, W. Icenogle, 5♂, 1♀ (DMNS ZA.25434).

Eremochelis oregonensis Brookhart and Cushing, 2002: **U.S.A.: Colorado:** *Hinsdale County*: 6 mi. N of Valley Falls, Hwy 31, Lake City, 26.v.1999, Opler and Buckner, holotype♂ (DMNS ZA.10008).

Eremorhax joshui (Brookhart and Muma, 1987): **U.S.A.: California:** *Kern County*: Dove Springs 2, 34.4237°N 118.0176°W, vi.2004, USGS-San Diego, 1♂ (DMNS ZA.16416). *San Bernardino County*: Marine Corps Air Ground, 34.2834°N 116.2998°W, vi.2000, USGS-San Diego, 1♀ (DMNS ZA.16415).

Hemerotrecha branchi Muma, 1951: **U.S.A.: California:** *San Bernardino County*: Wonder Valley, Amboy Road, 8.5 mi. E of 29 Palms, 34°09.942′N 115°54.203′W, 1600 m, 14.vii.2006, W. Icenogle, 2♂ (DMNS ZA.17234), 30–31.vii.2006, W. Icenogle, 1♂, 1♀ (DMNS ZA.16786).

Hemerotrecha cornuta Brookhart and Cushing, 2002: **U.S.A.: Colorado:** *Pueblo County*: Boone, 6 mi. NE, 38.310095°N 104.183558°W, 1504 m, 15.viii.1970, J.O. Brookhart, paratype♀ (DMNS ZA.17367), 20.vi.1976, J.O. Brookhart, holotype♂ (DMNS ZA.10005).

Hemerotrecha fruitanta Muma, 1951: **U.S.A.: Colorado:** *Arapahoe County*: Byers, 10 mi. SW, 39.61°N 104.36°W, 1722 m, 24.v.1974, J.O. Brookhart, 1♂ (DMNS ZA.17312), 1♀ (DMNS ZA.17313).

Hemerotrecha hanfordana Brookhart and Cushing, 2008: **U.S.A.: Washington:** *Franklin County*: Hanford National Monument, Wahlike Wildlife Area, White Bluff Ferry, 46°04.541″N 119°26.949″W, 21–28.vi.2002, R.S. Zack, holotype♂ (DMNS ZA.21371), 6–12.vii.2002, R.S. Zack, paratype♀ (DMNS ZA.19402).

Hemerotrecha marginata (Kraepelin, 1911): **U.S.A.: California:** *Los Angeles County*: San Pedro, vi.1907, 2♂, 2♀ syntypes (ZMUH [R8376]).

Hemerotrecha prenticei Brookhart and Cushing, 2008: **U.S.A.: California:** *Riverside County*: Multispecies Reserve (Lake Skinner), 22.3806°N 117.0022°W, 9–12.v.2000, T. Prentrice, holotype♂ (DMNS ZA.21376), 15–18.v.2000, T. Prentice, paratype♀ (DMNS ZA.21366).

Hemerotrecha sevilleta Brookhart and Cushing, 2002: **U.S.A.: New Mexico:** *Socorro County*: Sevilleta LTER Wild Fire Exp. Area, cell #11, 29.vi.1991, LTER staff, holotype♂ (DMNS ZA.10006), paratype♀ (DMNS ZA.10007).

Hemerotrecha vetteri Brookhart and Cushing, 2008: **U.S.A.: California:** *Santa Barbara County*: Vandenburg Air Force Base, 34.76°N

120.14°W, Abela, Pierce, and Pratt, holotype♂ (DMNS ZA.21377).

GALEODIDAE SUNDEVALL, 1833

Galeodes arabs C.L. Koch, 1842: **UNITED ARAB EMIRATES: Dubai Emirate:** Dubai Desert Conservation Reserve, 24°49′27.5″N 55°39′40.7″E, 17.vi.2003, P. Roosenschoon, 1♂ (AMNH [LP 9123]).

Galeodes araneoides (Pallas, 1772): **TURKEY: Iğdir Province:** Gürgen, 39°53′59.2″N 44°18′12.3″E, 889 m, 15.vi.2007, A.V. Gromov and H. Koç, 1♂, 1♀ (AMNH).

Galeodes olivieri Simon, 1879: **SENEGAL: Matam Province:** Ourosogui, 24 km N, 15°48′24.6″N 13°26′43.2″W, 41 m, 5.vii.2005, J. Huff and V. Vignoli, 1♀ (AMNH [LP 4628]). **Saint-Louis Province:** Ndioum, 16°30′48.2″N 14°39′50.5″W, 7 m, 6.vii.2005, J. Huff and V. Vignoli, 1♂ (AMNH [LP 4630]).

Galeodes toelgi Werner, 1922: **TURKEY: Hatay Province:** Ortaoba, 36°25′41.3″N 36°14′14.5″E, 200 m, 31.v.2007, A.V. Gromov, 1♂ (AMNH [LP 7536]).

Galeodes turkestanus Kraepelin, 1899: **UZBEKISTAN: Surkhandarya Area:** *Uzun District*: Dikhana Canyon, foothills of E slopes of Babatag Mountain Range, ca. 5 km WSW Akmechet village, 38°01.638′N 68°15.198′E, 722 m, 20–24.v.2003, L. Prendini and A.V. Gromov, 1♂, 1♀ (AMNH).

Galeodes spp.: **ISRAEL:** *Southern District*: Ashdod Nitzanim Nature Reserve, near Nitzan, 31°44′09.0″N 34°37′11.4″E, 17 m, 29.viii.2011, L. Prendini and T.L. Bird, 2♂ (AMNH [LP 11204]). **NIGER: Tahoua Department:** Birni N'kare, 120 km W, savannah, R. Brinckerhoff, 1♀ (MCZ).

Paragaleodes nesterovi Birula, 1916: **TURKEY: Şirnak Province:** Sinidagi Mt., 37°26′48.6″N 42°39′55.1″E, 26.vi.2007, A.V. Gromov and H. Koç, 1♂ (AMNH [LP 7480]).

Paragaleodes pallidus (Birula, 1890): **KAZAKHSTAN: South Kazakhstan Area:** *Otrar District*: Akkum, ca. 2–3 km W, 42°22′53″N 68°10′25″E, 202 m, 21.vi.2003, L. Prendini and A.V. Gromov, 1♂ (AMNH [LP 3922]).

Paragaleodes sp.: **ISRAEL:** *Southern District*: Sede Boqer, viii.2009, Y. Lubin, 1♀ (AMNH [LP 10550]).

GYLIPPIDAE ROEWER, 1933

GYLIPPINAE ROEWER, 1933

Gylippus (*Anoplogylippus*) *ferganensis* Birula, 1893: **UZBEKISTAN: Jizzax Area:** *Farish District*: Nuratau Nature Reserve: Nuratau Mountains, N slopes, ca. 1 km NW of Khayat village, 40°31′42″N 66°46′28″E, 978 m, 6–7.vi2003, A.V. Gromov, 1 juv. (AMNH [LP 3921]).

Gylippus (*Paragylippus*) *monoceros* Werner, 1905: **TURKEY: Isparta Province:** between Karamik and Sağir, 38°26.307′N 30°50.864′E, 1643 m, 13.v.2004, H. Koç, 1♂ (AMNH [LP 5437]). **Kayseri Province:** Lifos Mount, 38°35′22.8″N 35°27′59.4″E, 2100 m, 24.v.2013, M. Erdek, 1♀ (KUT).

LIPOPHAGINAE WHARTON, 1981

Bdellophaga angulata Wharton, 1981: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Gocheganas 26, 22°50′S 17°11′E, 1–20.vi.1981, S. Louw and M.-L. Penrith, 53♂ (NMNW 11601), 20–22.vi.1982, M.-L. Penrith, 18♂, 1♀ (NMNW 12240).

Lipophaga trispinosa Purcell, 1903: **SOUTH AFRICA: Western Cape Province:** *Prince Albert District*: Tierberg, old lands, 10.v.1990, West Cape Survey, W.R. Dean, 1♂ (NMNW 12503).

Trichotoma brunnea Lawrence, 1968: **NAMIBIA: Erongo Region:** *Swakopmund District*: Swakopmund, 30.v.2009, E. and B. Roxin, 1♀ (AMNH [LP 9870]).

Trichotoma michaelseni (Kraepelin, 1914): **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb, ca. 600 m N, 23°33′06″S 15°02′50″E, 395 m, 27.iii.2006, L. Prendini, T. Bird, and S.K. Uunona, 1♂ (AMNH [LP 5724]). **Karas Region:** *Lüderitz District*: Diamond Area 1: Sperrgebiet National Park: Scorpion Mine site, 27°49′S 16°35′E, 28.vii.1997, E. Griffin, 10♂, 1♀ (NMNW 12757); S of Bogenfels Arch, 27°27′36.2″S 15°23′38.6″E, 9 m, 14–16.vi.2008, C.M. Kaapehi and B. Muramba, 1♂ (NMNW).

Hexisopodidae Pocock, 1897

Chelypus hirsti Hewitt, 1915: **NAMIBIA: Hardap Region:** *Rehoboth District*: Farm Willies Rest 391, 10.vi.1966, C. van der Hoven, 2♂ (NMNW 10804). **Karas Region:** *Keetmanshoop District*: Farm Wildheim Ost 384, 1–30.iv.1977, S. Louw and M-L. Penrith (NMNW 11202).

Chelypus shortridgei Hewitt, 1931: **NAMIBIA: Karas Region:** *Lüderitz District*: Diamond Area 1: Sperrgebiet National Park: Obib Dunes, 27°53′S 16°32′E, 19.xi.1992, Huns Expedition, 1♂ (NMNW 12632).

Chelypus spp.: **NAMIBIA: Hardap Region:** *Mariental District*: Chulon, on Farm Narib Ost 602, Gibeon, M.J. and M.-L. Penrith, 16.v.1980, 1♂ (NMNW 11329). **Karas Region:** *Keetmanshoop District*: Tses, 25°55′12.5″S 18°10′54.5″E, R. Poller, F. van Deventer, J. Irish, and E. Marais, 4–7.iv.2003, 1♂ (NMNW 13475).

Hexisopus aureopilosus Lawrence, 1968: **NAMIBIA: Erongo Region:** *Karibib District*: Farm Emeritus 123, 1.vi.1967, Capt. Peterson, 1♀ (NMNW 11203).

Hexisopus lanatus (C.L. Koch, 1942): **NAMIBIA: Karas Region:** *Karasburg District*: Goodhouse, Warmbad, 14.xi.1963, L. Blom, 2♂ (NMNW 10795).

Hexisopus moiseli Lamoral, 1972: **NAMIBIA: Erongo Region:** *Karibib District*: Farm Emeritus 123, 9.vi.1967, Capt. Peterson, 1♂ (NMNW 10918).

Hexisopus psammophilus Wharton, 1981: **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb, 23°34′40.5″S 15°02′33.3″E, 412 m, 28–29.vii.2008, R.A. Wharton and T.L. Bird, 1♂ (AMNH [LP 9858]).

Hexisopus pusillus Lawrence, 1962: **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb, 2–14.v.1979, R.A. Wharton, 1♀ (NMNW 11426).

Hexisopus sp.: **NAMIBIA: Hardap Region:** *Maltahöhe District:* Zais, rocky hillside across from house, 27–29.ix.1985, E. Griffin, 9♂ (NMNW 13179). **Khomas Region:** *Windhoek District*: Farm Solitaire 412, 9.v.1975, E. Griffin, 1 juv. (NMNW 11098).

Karschiidae Kraepelin, 1899

Barrussus pentheri (Werner, 1905): **TURKEY: Kayseri Province:** *Hisarcik District*: Hisarcik, 38°36′44.7″N 35°31′09.5″E, 1739 m, 6–7.vii.2007, A.V. Gromov and E.A. Yağmur, 1 juv. (AMNH [LP 10693]).

Eusimonia divina Birula, 1935: **UZBEKISTAN: Navoiy Area:** *Tamdy District*: Kyzylkum Desert, foothills of Tamdytau Mountain Range, 2.5 km NW of Zarafshan, 41°35′47″N 64°11′05″E, 366 m, 3.vi.2003, L. Prendini and A.V. Gromov, 3♂, 7♀, 1 juv. (AMNH [LP 4098]).

Eusimonia furcillata (Simon, 1872): **ISRAEL:** *Southern District*: Sayeret Shaked, 11.ii.2007, 1♂ (HUJI 769).

Eusimonia nigrescens Kraepelin, 1899: **TURKEY: Mardin Province:** Yolbaşi, 37°16′00.8″N 40°48′00.0″E, 663 m, 26.v.2007, A.V. Gromov and H. Koç, 1♂ (AMNH [LP 7473]).

Eusimonia turkestana Kraepelin, 1899: **UZBEKISTAN: Fergana Area:** *Beshariq District*: Kairakkum sands/hills, 13 km WNW of Beshariq (Kirovo), 40°28.684′N 70°27.448′E, 365 m, 14.v.2003, L. Prendini and A.V. Gromov, 1♀ (AMNH [LP 4097]). **Khorezm Area:** *Hazorasp District*: Kyzylkum Desert, Uchizhak Hills, ca. 19 km N of Turpakkala, ca. 10 km E of Lebap [Turkmenistan], 41°01.673′N 62°00.361′E, 227 m, 31.v.2003, L. Prendini and A.V. Gromov, 1♂ (AMNH [LP 4096]).

Karschia (*Karschia*) *mastigofera* Birula, 1890: **TURKEY: Iğdir Province:** *Aralik District*: Yenidoğan, 39°47′12.3″N 44°23′36.9″E, 1563 m, 16.v–17.vi.2007, A.V. Gromov and H. Koç, 1♂ (AMNH [LP 7474]). **Van Province:** *Muradiye District*: Muradiye, 38°59′26.2″N 43°44′33.9″E, 1680 m, 19–20.vi.2007, A.V. Gromov and H. Koç, 2♀ (AMNH [LP 7476]).

Karschia (*Karschia*) *tibetana* Hirst, 1907: **TIBET:** *Lang County*: 22.vi.2004, Y. Ba and A. Shi, 1♂ (AMNH [LP 7719]).

Melanoblossiidae Roewer, 1933

Dinorhaxinae Roewer, 1933

Dinorhax rostrumpsittaci (Simon, 1877): **VIETNAM: Ba Ria-Vung Tau Province:** Binh Chau-Phuoc Buu Nature Reserve, 10°32′N 107°29′E, ca. 50 m, vi.2007, A.V. Abramov (expedition of Russia-Vietnam Tropical Centre), 1♂ (AMNH [LP 7537]). **Khan Hoa Province:** Cauda Nhatray [Cau Da Nha Trang], 28.x.1931, Dawydoff, 1♂ (MRAC).

Melanoblossiinae Roewer, 1933

Lawrencega minuta Wharton 1981: **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb dunes, 24.ix.1979, R.A. Wharton, 3♂, 1♀ (CAS 9033898).

Lawrencega procera Wharton, 1981: **NAMIBIA: Kunene Region:** *Khorixas District*: Farm Losberg 449, 6.7 km N intersection with D2612 on C35, 20°39′12.6″S 14°51′05.1″E, 888 m, 18.i.2009, T.L. Bird, J. Huff and L. Prendini, 1♂ (AMNH [LP 9863]).

Lawrencega tripilosa Lawrence, 1968: **SOUTH AFRICA: Northern Cape Province**: *Namaqualand District*: Richtersveld, Annisfontein, opposite Cornellskop, 23.xi.1975, E. Griffin, 1♂ (NMNW 11118).

Melanoblossia braunsi Purcell, 1903: **SOUTH AFRICA: Western Cape Province:** *Beaufort West District*: Farm Vaalkuil, Area 1, Site 4, 32.8139°S 22.7818°E, 3–6.xii.2007, D.H. Jacobs, 4♂, 1♀ (AMNH [LP 10737]).

Melanoblossia cf. *braunsi*: **SOUTH AFRICA: Northern Cape Province:** *Calvinia District*: Farm Springbokpan (Springboktand), N of Loeriesfontein, 30°23′23″S 19°24′09″E, 5–12.x.2006, M. Burger, D. Massyn, and J. Sakwa, 1♂ (AMNH [LP 8550]).

Melanoblossia sp.: **NAMIBIA: Karas Region:** *Lüderitz District*: Diamond Area 1: Sperrgebiet National Park: Tsaukhaib Mountain, old transport route, 26°42′58.0″S 15°40′12.6″E, 906 m, 24–30.viii.2006, EduVentures 9 Expedition, 1♂ (AMNH [LP 9857]), 1♂ (NMNW 13392), 3♂ (NMNW 13394), 1♂ (NMNW 13395); 5♂ (NMNW 13396), 4♂ (NMNW 14179).

Mummuciidae Roewer, 1934

Gaucha fasciata Mello-Leitão, 1924: **URUGUAY: Rivera Department:** Route 30, km 233, ca. 100 km SE of Artigas, 31°08′25.692″S 55°55′11.280″W, 345 m, 13.xii.2005, C.I. Mattoni, A.A. Ojanguren-Affilastro, and F. Labarque, 1♂ (AMNH [LP 5858]), 1♀ (AMNH [LP 10699]).

Uspallata cf. *pulchra*: **CHILE: Region IV (Coquimbo):** *Elqui Province*: Mangueras, Mina el Indio, ca. 4200 m, 7.xi.2003, L. Prendini, C.I. Mattoni, and J.A. Ochoa, 28♂ (AMNH [LP 2403]).

Rhagodidae Pocock, 1897

Rhagoderma tricolor Roewer, 1941: **TURKEY: Gaziantep Province:** *Gaziantep District*: Yedi Tepe M. Sehir ici Sahinbey, G. Antep, 1.vii.2005, E.A. Yağmur, 1♂ (AMNH [LP 5435]).

Rhagodes melanus (Olivier, 1807): **EGYPT:** vii.2003, 1♂ (AMNH [LP 2293]). **ISRAEL:** *Southern District*: Agur sand dunes, near Egyptian border, viii.2009, B. Shacham, 1♀ (AMNH [LP 10549]), 5♂, 1♀ (NMNW 14226).

Rhagodes sp.: **KENYA: Rift Valley Province:** Kalabata River where Lokori–Lodwan road crosses SE of Loperot, Turkana, 30.vi–26.vii.1965, B. Patterson Expedition, 1♂ (MCZ 126321).

Solpugidae Leach, 1815

Ferrandiinae Roewer, 1933

Ferrandia robusta Lawrence, 1954: **SOMALIA: Toghdeer Province:** Burao, P.E. Glovere, 1♀ (MCZ 126329).

Solpuginae Leach, 1815

Metasolpuga picta (Kraepelin, 1899): **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb plains, 16.xi.1979, V. Gray, 1 subad.♂ (AMNH); Gobabeb, 23°34′40.5″S 15°02′33.3″E, 412 m, 28–29. vii.2008, R.A. Wharton and T.L. Bird, 1♂ (AMNH [LP 10719]).

Oparba asiatica (Turk, 1948): **EGYPT: Ismailia Governate:** Qassassin, vi.1942, Buxton, holotype♂ (HUJI). **Sinai Governate:** Sheikh el Karai, Sinai, 8.iv.1968, 1♂ (HUJI 360). **ISRAEL:** *Southern District*: Ezuz, 22.iv.2012, A. Novikova, 1♂ (HUJI 684); Negev, Retanim, 2.vii.2012, S. Aharon, 1♂ (TAUZM 50313).

Oparbella flavescens (C.L. Koch, 1842): **TUNISIA: Tunis Governate:** Tunis, Central-gebirge, N. Banks, 1♂, 1♀ (MCZ 102912).

Oparbella sp.: **MOROCCO: Guelmim-Es Semara Region:** *Tata Province*: Tata, 14.ii.2007, R. Bosmans, 1♂ (MRAC 230.211).

Prosolpuga schultzei (Kraepelin, 1908): **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Homeb, 23°38.785′S 15°11.424′E, 409 m, 30.xii.2003, L. Prendini and E. Scott, 1♀, 1 juv. (AMNH [LP 3605]). **Karas Region:** *Lüderitz District*: Diamond Area 1: Sperrgebiet National Park: E of Oranjemund, 8–11.xi.1986, E. Griffin, 3♂ (NMNW 13759).

Solpuga chelicornis Lichtenstein, 1796: **SOUTH AFRICA: Northern Cape Province:** *Britstown District*: Farm Kareebosch Poort, 0.9 km SE railway intersection with N10 (Prieska–Britstown) on gravel road (Voëlgeraas–Broken Dam), 30°26.831′S 23°21.883′E, 1066 m, 30. xii.2007, L. Prendini and M. Cooper, 1♂ (AMNH [LP 8158]).

Solpuga c. carlkochi Harvey, 2002: **SOUTH AFRICA: Western Cape Province:** *Beaufort West District*: Farm Vaalkuil, Area 1, Site 4, 32.8139°S 22.7818°E, 3–6.xii.2007, D.H. Jacobs, 1♂ (AMNH [LP 10285]), 1♀ (NCA 2008/3524).

Solpuga massaica Roewer, 1941: **TANZANIA: Arusha Region:** Massai Steppe, East Africa, 1♂, 1 subad.♂ syntypes (SMF 9907391 [RII/7391/450]).

Solpuga roeweri Fage, 1936: **KENYA: Rift Valley Province:** Loperot, viii.1964, B. Patterson, 1♂, 1 juv. (MCZ 126317).

Solpugassa furcifera (Kraepelin, 1899): **NAMIBIA: Kunene Region:** *Opuwo District*: Ohopoho [Opuwo], viii.1956, C. Koch, holotype♂ [*Solpugassa kochi* Lawrence, 1959] (TMSA 8843); Puros, 5 km N, on E side of Hoarusib riverbed, at W edge of Etendeka Mountains, 18°43.461′S 12°56.879′E, 320 m, 19.i.2004, L. Prendini, E. Scott, T.L. and C. Bird, Q. and N. Martins, 3♂, 2♀ (AMNH [LP 3632]).

Solpugella asiatica Roewer 1933: **ISRAEL: Gaza:** vi.1942, 1♀ (HUJI).

Solpugella sp.: **ANGOLA: Cunene Province:** *Cahama Municipality*: Cahama, 15 km E of Cunene River, 4–6.xii.1974, M.-L. Penrith, 1♂ (NMNW 11097).

Solpugema brachyceras (Lawrence, 1931): **SOUTH AFRICA: Western Cape Province:** *Paarl District*: Mont Rochelle Nature Reserve, Perdekop trail, Franschhoek, 33°54.102′S 19°09.531′E, 5.xi.2000, L. Prendini, E. Scott, R. and K. Lynch, 1♂ (AMNH [LP 1960B]).

Solpugema derbiana (Pocock, 1895): **SOUTH AFRICA: Northern Cape Province:** *Hay District*: Farm Boseekoebaard, SE of Groblershoop, 29°02′00″S 22°17′19″E, 4–13.xii.2005, M. Burger, H. Janse van Vuuren, C. Lyons, and S. Ward, 1♂ (AMNH [LP 7709]).

Solpugema genucornis (Lawrence, 1935): **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Holoog 106 (Holoog boma site), 27.41098°S 17.96102°E, 809 m, 29.i.2009, R. and D.R. Brand, 1♀ (AMNH [LP 10292]). **SOUTH AFRICA: Northern Cape Province:** *Namaqualand District*: Farm Gemsbokvlei 571, 7.8 km N turnoff from R382 (Port Nolloth–Steinkopf) on road to Lekkersing, 29°15.16′S 17°06.377′E, 181 m, 3.i.2008, L. Prendini and M. Cooper, 1♂ (AMNH [LP 8167]).

Solpugema hamata (Hewitt, 1914): **SOUTH AFRICA: Mpumalanga Province:** *Barberton*

District: Barberton, xii.1922, G.P.F. van Dam, 1♂ (TMSA 6632 old 856).

Solpugema hostilis (White, 1846): **SOUTH AFRICA:** Transvaal, 1♂, 1♀ (SMF [R3117]). **KwaZulu-Natal Province:** *Ubombo District*: iSimangaliso Wetland Park, Mkuze Game Reserve, 27°38′S 32°14′E, 16.vii.2007, C. Smith, 1♂ (NCA 2009/2817).

Solpugema intermedia (Lawrence, 1929): **SOUTH AFRICA: Western Cape Province:** *Laingsburg District*: Anysberg Nature Reserve, 33°28.759′S 20°34.610′E, 9–13.xii.2008, R. Lyle, D. du Plessis, H. van As, V. Butler, and J. Terblanche, 1♂ (AMNH [LP 10249]), 1♂ (NCA 2009/4482).

Solpugema montana (Lawrence, 1929): **SOUTH AFRICA: Western Cape Province:** *Worcester District*: Matroosberg Mountains, syntype♂ (SMF 9902904 [RII/2904/32]).

Solpugema phylloceras (Lawrence, 1929): **SOUTH AFRICA: Northern Cape Province:** *Heidelberg District*: Grootvadersbosch, ix.1940, V. Fitzsimons, 1♂ (TMSA 8606).

Solpugema tubicen (Kraepelin, 1911): **SOUTH AFRICA:** 1♂ (TMSA 2643 old 769); Transvaal, 1910, 1♂, 2♀ syntypes (ZMUH [R9503]).

Solpugiba lineata (C.L. Koch, 1842): **NAMIBIA: Hardap Region:** *Maltahöhe District*: Namib Rand Nature Reserve: Farm Aandster 147, 25°22′04.14″S 16°04′56.04″E, 2.i.2000, E. Griffin, 2♂ (NMNW 13814). **SOUTH AFRICA: Northern Cape Province:** *Hay District*: Farm Koedoesnek, E of Langberge, ENE of Groblershoop, 28°46′27″S 22°31′01″E, 14–22.xii.2005, M. Burger, D. du Toit, and R. James, 2♂, 1♀, 2 juv (AMNH [LP 5919]).

Solpugista hastata (Kraepelin, 1899): **NAMIBIA:** Groß Namaqualand, holotype♂ [chelicera only] (SMF [R6918]).

Solpugista bicolor (Lawrence, 1953): **NAMIBIA: Erongo Region:** *Swakopmund/Karibib Districts*: Swakopmund to Usakos, 14.ix.2007, J. Visser, 1♂ (AMNH [LP 7933]). *Swakopmund District*: Namib-Naukluft Park: Gorob mine, 23°34′11.6″S 15°15′29.1″E, 603 m, 20.i.2009, T.L. Bird, J. Huff, and L. Prendini, 1♀ (AMNH [LP 9879]).

Solpugisticella kenyae Turk, 1960: **KENYA:** holotype♂ (HUJI).

Solpuguna alcicornis (Kraepelin, 1914): **NAMIBIA: Karas Region:** *Keetmanshoop District*: Keetmanshoop, viii.1912, W. Krause, 1♂, 1♀ (ZMUH [R8515]).

Solpuguna collinata (Purcell, 1903): **SOUTH AFRICA: Northern Cape Province:** *Namaqualand District*: Richtersveld National Park: Koegavlakte, Richtersveld, 7.xi.2009, M. Uhlig and K. Ebert, 1♂ (AMNH [LP 10247]), 3♂ (NCA 2009/4494).

Solpuguna cf. *orangica*: **SOUTH AFRICA: Northern Cape Province:** *Prieska District*: Farm Good Hope, ca. 30 km SW of Prieska, 29°51′38″S 22°31′29″E, 9–18.i.2006, M. Burger, D. Haarmeyer and D. Massyn, 2♂, 1♀ (AMNH [LP 5969]).

Solpugyla sp.: **MALAWI: Southern (Blantyre) Region:** *Balaka District*: Liwonde National Park: Chinguni Hills Camp (Chinguni Lodge), at base Mount Chinguni, 15°00′49″S 35°15′40″E, 519 m, 12.xii.2007, L. Prendini and W.R. Schmidt, 5♂, 3♀ (AMNH [LP 10764]). **MOZAMBIQUE: Tete Province:** *Tete District*: Tete, close to top of hill with communications tower overlooking town, 16°12′01.7″S 33°33′57.9″E, 400 m, 9–10.xii.2007, L. Prendini and W.R. Schmidt, 1♂ (AMNH [LP 8138]).

Zeria adunca (Roewer, 1933): **ZAMBIA: Northern Province:** *Mpulungu District*: Mpulungu, Nkupi Lodge, 24.x.2001, J. Snoeks and M. Hansens, 1♂ (MRAC 216.105).

Zeria carli (Roewer, 1933): **MOZAMBIQUE: Maputo Province:** *Matutuine District*: Blue Anchor Inn, near Marracuene, 25°35.124′S 32°39.568′E, 50 m, 28.xi.2007, C. Haddad and R. Fourie, 1♂ (AMNH [LP 7915]).

Zeria fordi (Hirst, 1907): **KENYA: Rift Valley Province:** Lake Bogoria National Reserve: Chemurak Valley, 00.355250°S 36.064944°E, 27.iv.2007, K. Reddick and J. Mugambi, 1♂ (AMNH [LP 9090]).

Zeria fusca (C.L. Koch, 1842): **SOUTH AFRICA: Western Cape Province:** *Wynberg District*: Newlands Forest, x.1997, L. Prendini, E. Scott, and J. Knight, 1♂ (AMNH [LP 1473]); Newlands Forest, E slope Table Mountain, 26.xi.2000, L. Prendini and E. Scott, 2♀ (AMNH [LP 1472]).

Zeria glabricornis (Lawrence, 1928): **NAMIBIA: Kunene Region:** *Opuwo District*: Ruacana, 5 km NNE, 17°25.869′S 14°21.522′E, 1109 m, 6.i.2004, L. Prendini, E. Scott, T.L. and C. Bird, Q. and N. Martins, 1♂ (AMNH [LP 3614]).

Zeria keyserlingi (Pocock, 1895): **GUINEA-BISSAU: Bafat**á **Region:** Bambadinca, property of Riverzoo Farm, 12°00′09.0″N 14°53′25.9″W, 28 m, 29.vi–2.vii.2005, J. Huff and V. Vignoli, 1♂ (AMNH [LP 4632]).

Zeria lawrencei (Roewer, 1933): **NAMIBIA: Hardap Region:** *Maltahöhe District*: Namib-Naukluft Park: Sossusvlei, Elim Dune, 24°27′35.0″S 15°46′33.2″E, 827 m, 2.xi.2009, T.L. Bird, J. Huff, and L. Prendini, 1♂ (AMNH [LP 9906]), 2♂, 1♀ (NMNW 13820).

Zeria sericea (Pocock, 1897): **NAMIBIA: Otjozondjupa Region**: *Grootfontein District*: Farm Uisib 427, 19°33′19.9″S 17°11.53.3″E, 1343 m, 31.xii.2008, T.L. Bird, J. Lukas, and K. Schoeman, 7♂, 1♀ (NMNW 13801), 19°32′54.1″S 17°14.06.8″E, 1343 m, 29.xii.2008-2.i.2009, T.L. and C. Bird, and K. Schoeman, 6♂ (NMNW 13800).

Zeria strepsiceros (Kraepelin, 1899): **MOZAMBIQUE: Maputo Provice:** *Matutuine District*: Delagoa Bay, 7.x.1893, W. Joost, holotype♂ (ZMUH [R9500]).

Zeria venator (Pocock, 1897): **SOUTH AFRICA: Northern Cape Province:** *Britstown District*: Farm De Put, ca. 30 km SE of Britstown, 30°48′53″S 23°40′58″E, 20–29.i.2006, M. Burger, M. Carstens, K. Jacobs, and A. Pretorius, 3♂, 1♀ (AMNH [LP 5952]). **NAMIBIA: Karas Region:** *Karasburg District*: Farm Ortmansbaum 120, on banks of Ortmans River, 28°18′S 18°43′E, 26.i.1973, B.H. Lamoral and L. Raw, 5♂, 2♀ (NMSA 16273).

Zeria sp.: **KENYA: Eastern Province:** *Kibwezi District*: Tsavo National Park, Kitani Lodge, 2♂ 2♀ (CAS).

Zeriassa cf. *furcicornis*: **NAMIBIA: Otjozondjupa Region:** *Grootfontein District*: Farm Uisib 427, red sandy flats in valley, 19°32′54.3″S 17°14′08.8″E, 1340 m, 3.i.2004, L. Prendini, E. Scott, T.L. and C. Bird, Q. and N. Martins, 1♂ (AMNH [LP 3612]), 19°32′54.1″S 17°14′06.8″E, 1343 m, 29.xii.2008–2.i.2009, T.L. and C. Bird, and K. Schoeman, 1 juv. (AMNH [LP 9848]).

Zeriassa sp.: **KENYA: Rift Valley Province:** Kalabata River where Lokori–Lodwan road crosses SE of Loperot, Turkana, 30.vi–26.vii.1965, B. Patterson Expedition, 1 juv. (MCZ ex 126321); Kanebi, Pleist., 27.vii–8.viii.1965, B. Patterson Expedition, 1♀, 1 juv. (MCZ 126318).

PLATES

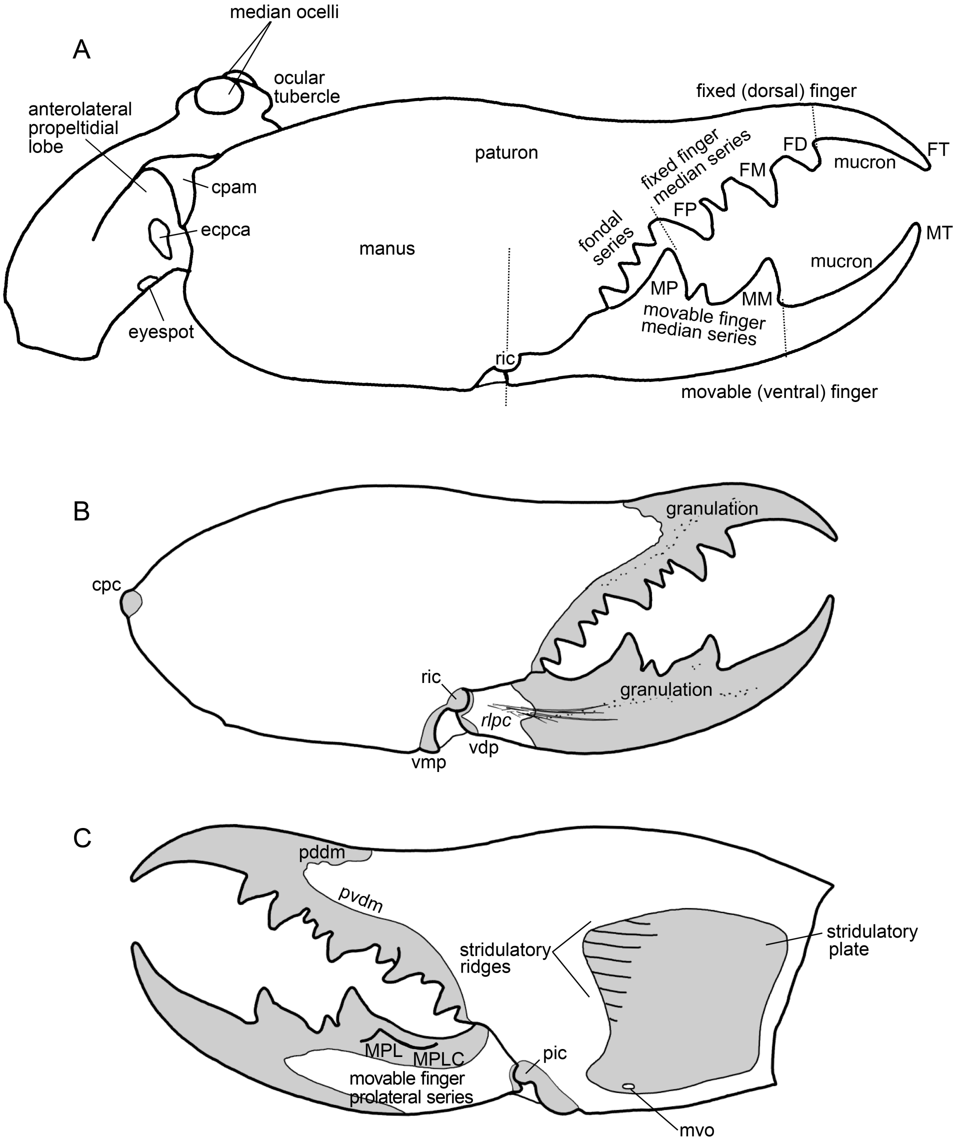

A
median ocelli
ocular tubercle
anterolateral propeltidial lobe
fixed (dorsal) finger
paturon
fixed finger median series
FD
FT
mucron
FM
cpam
FP
ecpca
fondal series
MT
manus
mucron
MP
MM
movable finger median series
eyespot
ric
movable (ventral) finger
B
granulation
cpc
ric
granulation
rlpc
vdp
vmp
C
pddm
pvdm
stridulatory ridges
stridulatory plate
MPL
MPLC
pic
movable finger prolateral series
mvo

PLATE 1. Solpugidae Leach, 1815, female cheliceral morphology. **A.** *Zeria lawrencei* (Roewer, 1933), ♀ (NMNW 13820), chelicera and propeltidium, lateral view, illustrating attachment to propeltidium via cheliceropeltidial articulation site involving cheliceropeltidial condyle (visible as pale spot on retrolateral surface) and articular membrane. **B, C.** *Solpugassa furcifera* (Kraepelin, 1899), ♀ (AMNH [LP 3632]), chelicerae, retrolateral (**B**) and prolateral (**C**) views. Grey shading denotes asetose areas. Abbreviations: **cpam,** cheliceropeltidial articular membrane; **cpc,** cheliceropeltidial condyle; **ecpca,** external cheliceropeltidial condylar attachment; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FT,** fixed finger, terminal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MPLC,** movable finger, prolateral carina; **MT,** movable finger, terminal tooth; **mvo,** medioventral organ; **pic,** prolateral interdigital condyle; **pddm,** asetose area, prodorsal distal margin; **pvdm,** asetose area, proventral distal margin; **ric,** retrolateral interdigital condyle; ***rlpc*,** retrolateral proximal setal cluster; **vdp,** ventral digital plagula; **vmp,** ventral manus plagula.

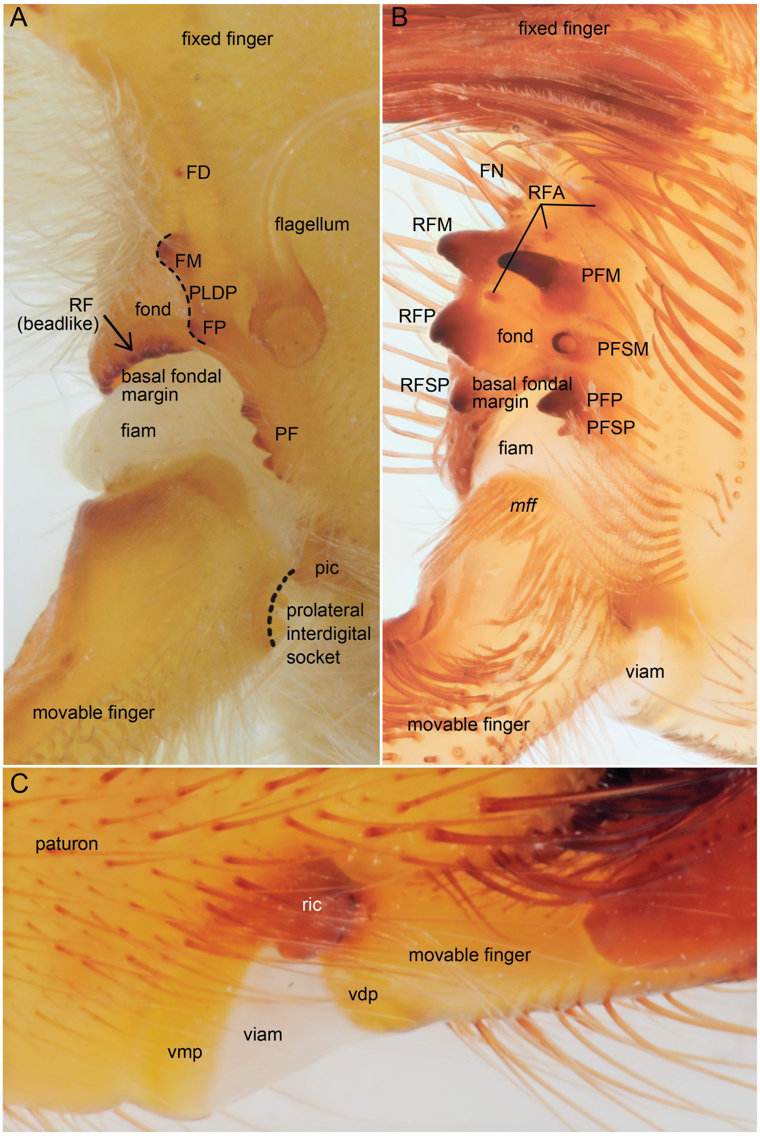

A
fixed finger
FD
flagellum
FM
PLDP
RF
(beadlike)
fond
FP
basal fondal
margin
fiam
PF
pic
prolateral
interdigital
socket
movable finger
B
fixed finger
FN
RFA
RFM
PFM
RFP
fond
PFSM
RFSP
basal fondal
margin
PFP
PFSP
fiam
mff
viam
movable finger
C
paturon
ric
movable finger
vdp
viam
vmp

PLATE 2. Hexisopodidae Pocock, 1897 (**A**), Eremobatidae Kraepelin, 1899 (**B**), and Solpugidae Leach, 1815 (**C**), cheliceral fond and interdigital articulation. **A.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795), modified fondal area, prodistal view. Dashed line indicates movable finger, prolateral interdigital socket. **B.** *Eremobates palpisetulosus* Fichter, 1941, ♂ (DMNS ZA.15683), modified fondal area, prodistal view. **C.** *Solpugyla* sp., ♀ (AMNH [LP 10764]), movable finger attachment to paturon, retrolateral view, illustrating ventral interdigital articulation. Abbreviations: **FD,** fixed finger, distal tooth; **fiam,** fondal interdigital articular membrane; **FM,** fixed finger, medial tooth; **FN**, fondal notch; **FP**, fixed finger, proximal tooth; ***mff***, movable finger, fondal setae; **PF,** profondal teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **pic,** prolateral interdigital condyle; **PLDP,** prolateral dental process; **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth; **ric,** retrolateral interdigital condyle; **vdp,** ventral digital plagula; **viam,** ventral interdigital articular membrane; **vmp,** ventral manus plagula.

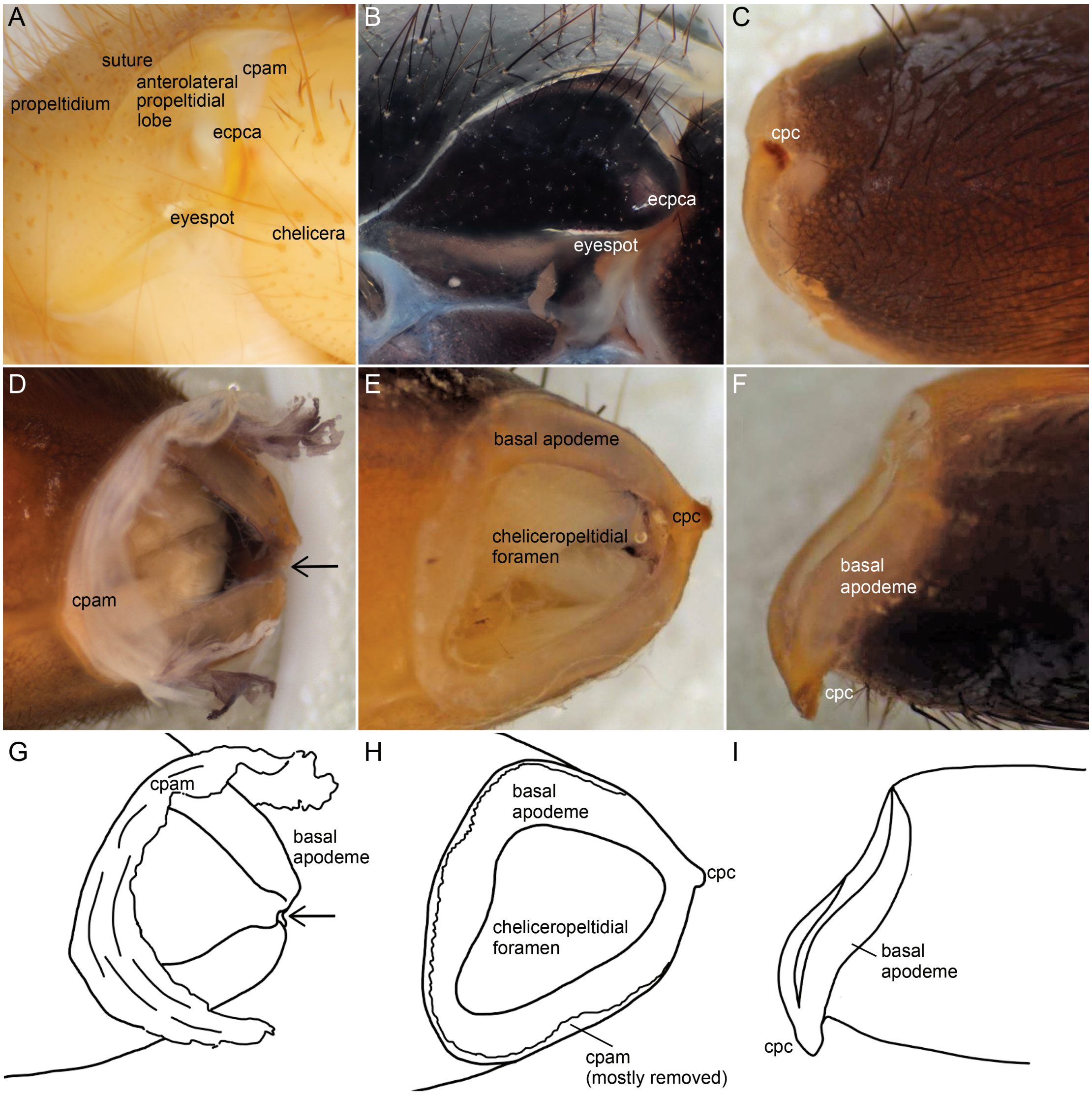

A
suture
cpam
anterolateral
propeltidium
propeltidial
lobe
ecpca
eyespot
chelicera
B
ecpca
eyespot
C
cpc
D
cpam
E
basal apodeme
cpc
cheliceropeltidial
foramen
F
basal
apodeme
cpc
G
cpam
basal
apodeme
H
basal
apodeme
cpc
cheliceropeltidial
foramen
cpam
(mostly removed)
I
basal
apodeme
cpc

PLATE 3. Solpugidae Leach, 1815 (**A**) and Rhagodidae Pocock, 1897 (**B–I**), cheliceropeltidial articulation. **A.** *Zeria lawrencei* (Roewer, 1933), ♀ (NMNW 13820), cheliceral attachment to propeltidium, lateral view. **B–F.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW 14226), cheliceral attachment to propeltidium, lateral view (**B**) and chelicera removed from propeltidium, retrolateral view, illustrating basal area of articulation (**C**); prolateral view, membrane that connects chelicera to prosoma attached (**D, G**); prolateral proximal view, articular membrane removed, illustrating condyle, cheliceral foramen and basal apodeme (**E, H**); dorsal view, illustrating condyle projecting retrolaterally (**F, I**). Arrows indicate position of **cpc**. Abbreviations: **cpam,** cheliceropeltidial articular membrane; **cpc,** cheliceropeltidial condyle; **ecpca,** external cheliceropeltidial condylar attachment.

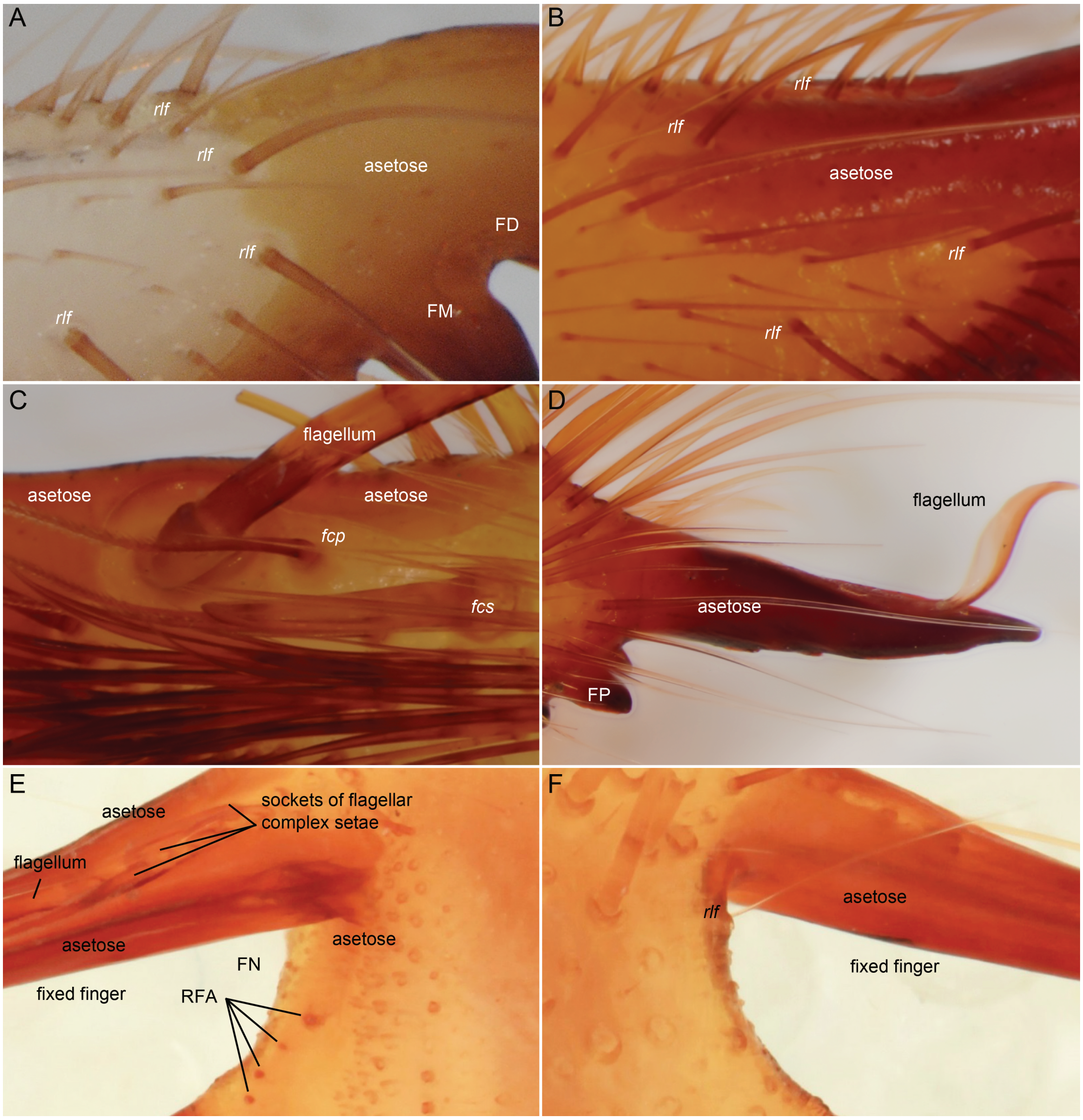

A
rlf
rlf
asetose
FD
rlf
FM
rlf
B
rlf
rlf
asetose
rlf
rlf
C
flagellum
asetose
asetose
fcp
fcs
D
flagellum
asetose
FP
E
asetose
sockets of flagellar complex setae
flagellum
asetose
asetose
FN
fixed finger
RFA
F
rlf
asetose
fixed finger

PLATE 4. Ceromidae Roewer, 1933 (**A**), Galeodidae Sundevall, 1833 (**B, C**), Gylippinae Roewer, 1933 (**D**), and Eremobatidae Kraepelin, 1899 (**E, F**), cheliceral fixed finger, retrolateral (**A, B, D, F**), and prolateral (**C, E**) views, illustrating asetose area curving around bases of retrolateral finger (*rlf*) setae (**A, B**) or around base of flagellum (**C**), apparent origin of flagellum on asetose area (**D**), and setose area reduced to narrow strip with flagellar complex setae situated therein, and asetose area reduced to narrow strip, situated slightly prolateral in fondal notch (**E**), and with setae situated in fondal notch but not on asetose area (**F**). **A.** *Ceroma inerme* Purcell, 1899, ♀ (AMNH [LP 8425]). **B.** *Galeodes araneoides* (Pallas, 1772), ♀ (AMNH), Turkey: Gurgen. **C.** *Galeodes olivieri* Simon 1879, ♂ (AMNH [LP 4630]). **D.** *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **E, F.** *Eremobates chihuaensis* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10002). Abbreviations: ***fcp*****,** flagellar complex plumose seta(e); ***fcs*****,** flagellar complex spiniform setae; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FN,** fondal notch; **FP,** fixed finger, proximal tooth; **RFA,** retrofondal apical teeth; ***rlf*****,** retrolateral finger setae.

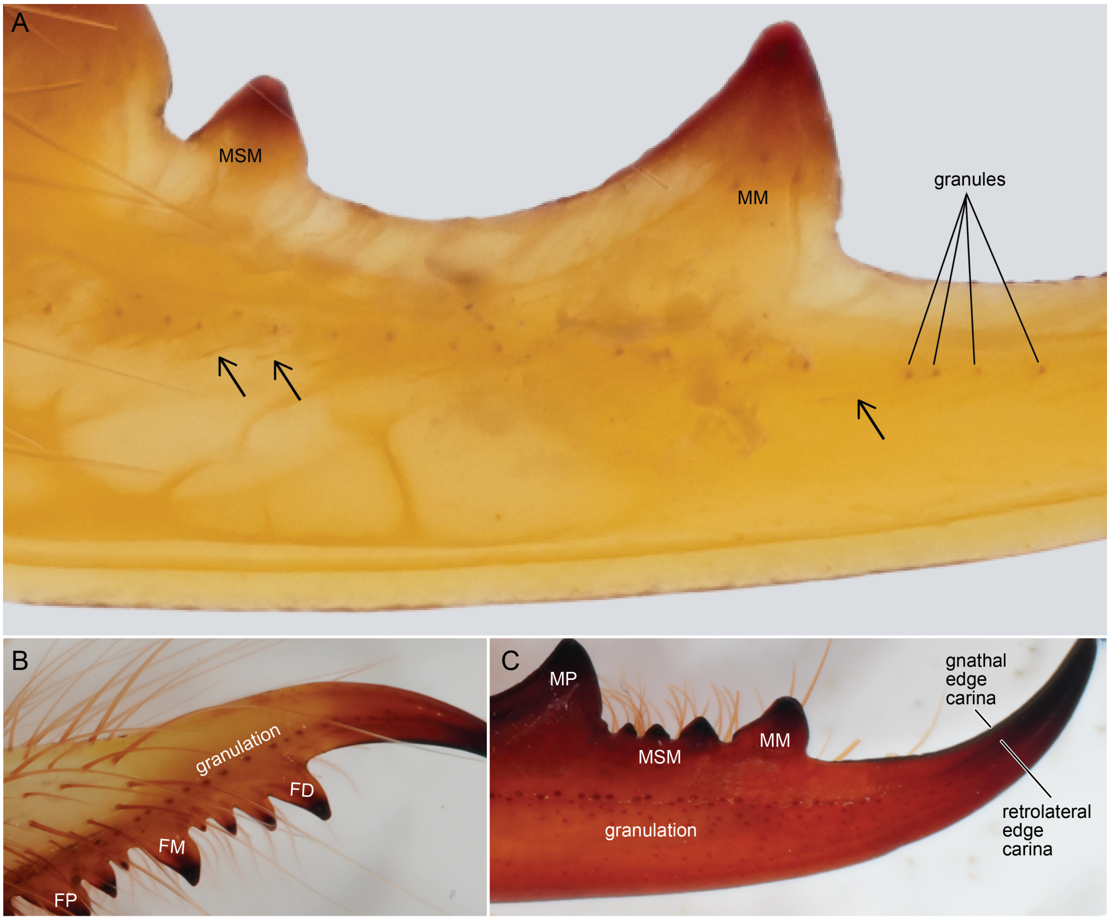

A
MSM
MM
granules
B
granulation
FD
FM
FP
C
MP
MSM
MM
granulation
gnathal edge carina
retrolateral edge carina

PLATE 5. Solpugidae Leach, 1815 (**A**), Daesiidae Kraepelin, 1899 (**B**), and Galeodidae Sundevall, 1833 (**C**), cheliceral fingers, retrolateral views, illustrating asetose areas. **A.** *Metasolpuga picta* (Kraepelin, 1899), subad. ♂ (AMNH), Namibia: Gobabeb, movable finger, illustrating fine canals (arrows) terminating in "granules." **B.** *Namibesia pallida* Lawrence, 1962, ♀ (AMNH [LP 4017]), fixed finger, illustrating prominent granular row. **C.** *Galeodes araneoides* (Pallas, 1772), ♀ (AMNH), Turkey: Gurgen, movable finger, illustrating sparse, scattered "granules" in addition to prominent granular row. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth.

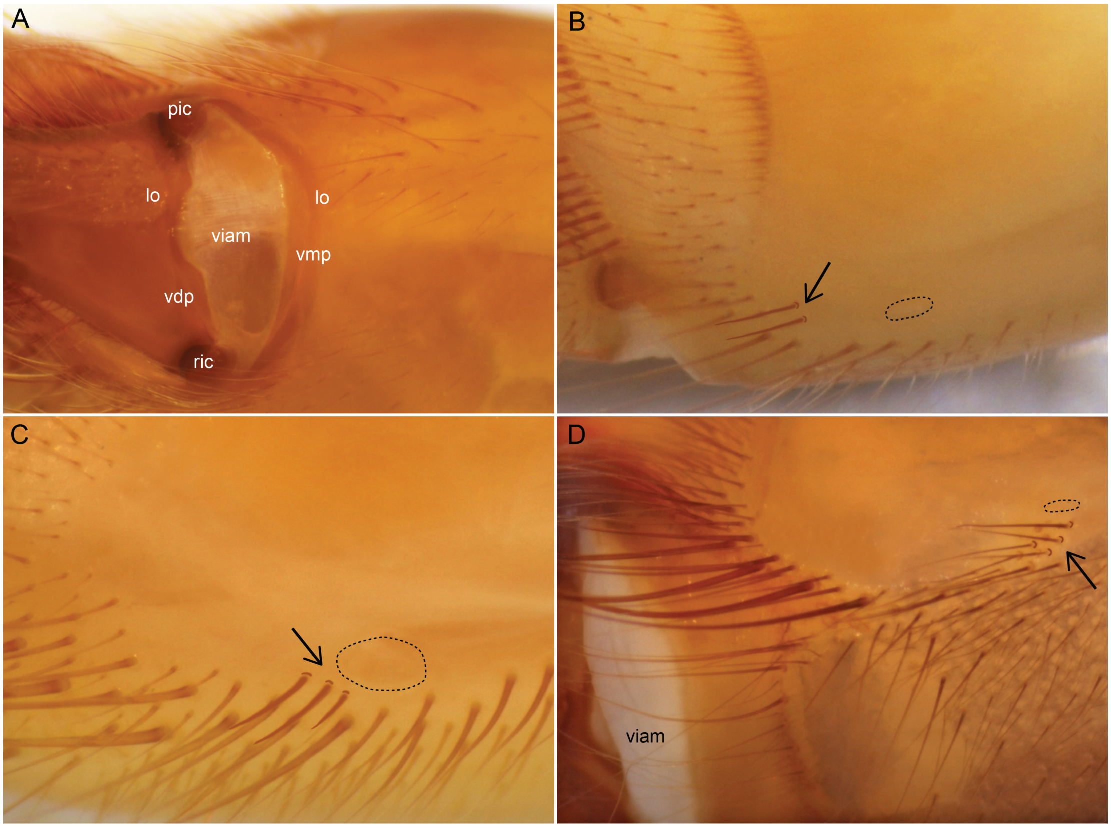


PLATE 6. Solpugidae Leach, 1815 (**A, B**), Galeodidae Sundevall, 1833 (**C**), and Rhagodidae Pocock, 1897 (**D**), chelicerae, interdigital articulation, ventral view (**A**), and manus, prolateral views (**B–D**), illustrating putative sensory organs. **A.** *Solpuga chelicornis* Lichtenstein, 1796, ♂ (AMNH [LP 10285]). **B.** *Oparbella* sp., ♂ (MRAC 230.211). **C.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 7536]). **D.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW 14226). Dotted lines indicate medioventral organ (mvo). Arrows indicate setae probably associated with medioventral organ. Abbreviations: **lo,** lyriform organ; **mvo,** medioventral organ; **pic,** prolateral interdigital condyle; **ric,** retrolateral interdigital condyle; **vdp,** ventral digital plagula; **viam,** ventral interdigital articular membrane; **vmp,** ventral manus plagula.

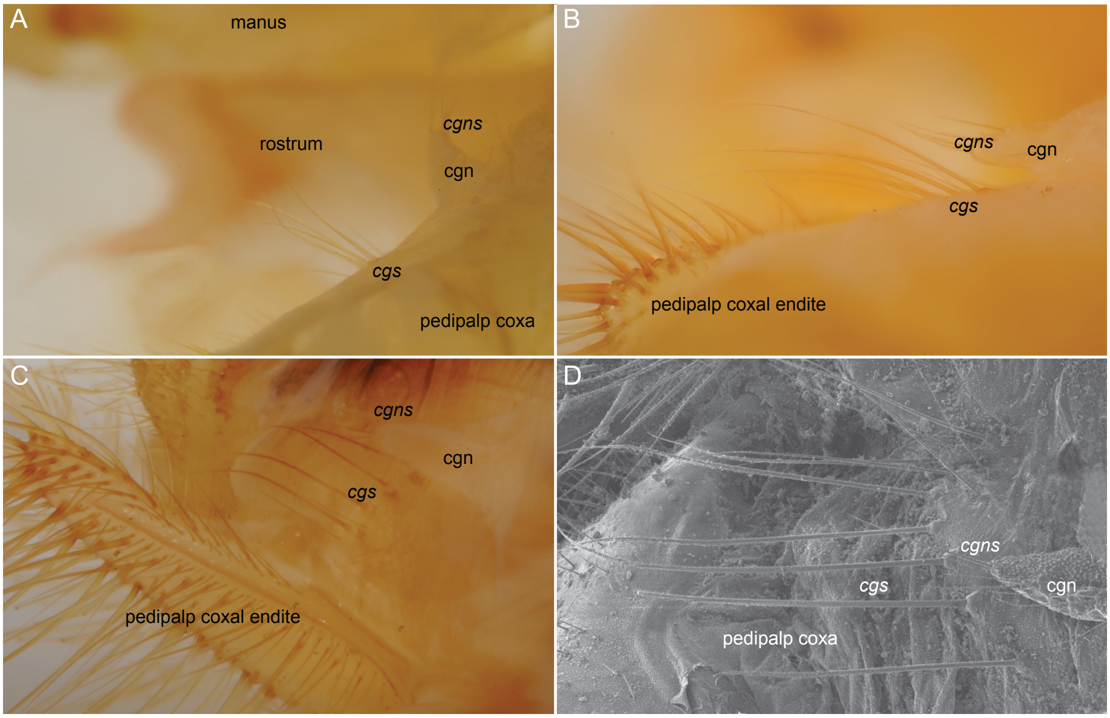

A
manus
rostrum
cgns
cgn
cgs
pedipalp coxa
B
cgns
cgn
cgs
pedipalp coxal endite
C
cgns
cgn
cgs
pedipalp coxal endite
D
cgns
cgs
cgn
pedipalp coxa

PLATE 7. Galeodidae Sundevall, 1833 (**A**), Ceromidae Roewer, 1933 (**B**), Solpugidae Leach, 1815 (**C**), and Lipophaginae Wharton, 1981 (**D**), pedipalpal coxae, dorsal surfaces, lateral (**A, B**) and dorsal (**C, D**) views (anterior at left), illustrating anterodorsal projection of coxal gland papillae and setae, bringing structure in contact with ventral surface of chelicera. **A.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]). **B.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **C.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). **D**. *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601). Abbreviations: **cgn,** coxal gland nozzle; ***cgns*,** coxal gland nozzle setae; ***cgs*,** coxal gland setae.

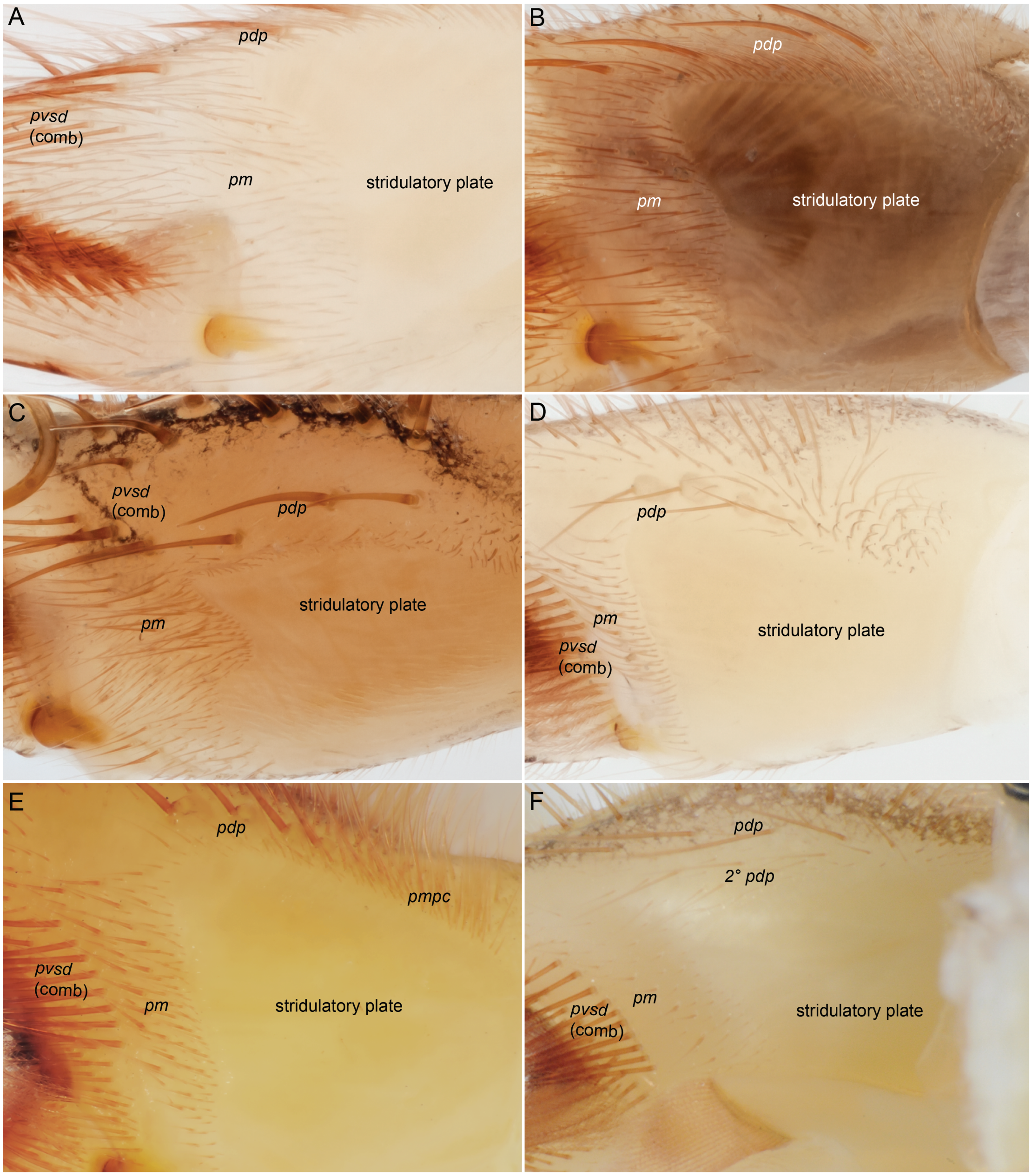

A
pdp
pvsd
(comb)
pm
stridulatory plate
B
pdp
pm
stridulatory plate
C
pvsd
(comb)
pdp
pm
stridulatory plate
D
pdp
pm
pvsd
(comb)
stridulatory plate
E
pdp
pmpc
pvsd
(comb)
pm
stridulatory plate
F
pdp
2° pdp
pvsd
(comb)
pm
stridulatory plate

PLATE 8. Karschiidae Kraepelin, 1899 (**A–C**), Gylippinae Roewer, 1933 (**D, E**), and Ceromidae Roewer, 1933 (**F**), chelicerae, prolateral views, illustrating differences in stridulatory apparatus with weak to absent ridges, field of promedial (***pm***) setae with unmodified to weakly modified stridulatory setae, prodorsal proximal (***pdp***) setae, comb of proventral subdistal (***pvsd***) setae (situated dorsally in **A, C**), and setiform promedial proximal setal cluster (***pmpc***). **A.** *Eusimonia turkestana* Kraepelin, 1899, ♀ (AMNH [LP 4097]). **B.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♀ (AMNH [LP 7476]). **C.** *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **D.** *Gylippus* (*Anoplogylippus*) *ferganensis* Birula, 1893, juv. (AMNH [LP 3921]). **E.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **F.** *Ceroma inerme* Purcell, 1899, ♂ (AMNH [LP 9864]). Abbreviation: **2°,** secondary.

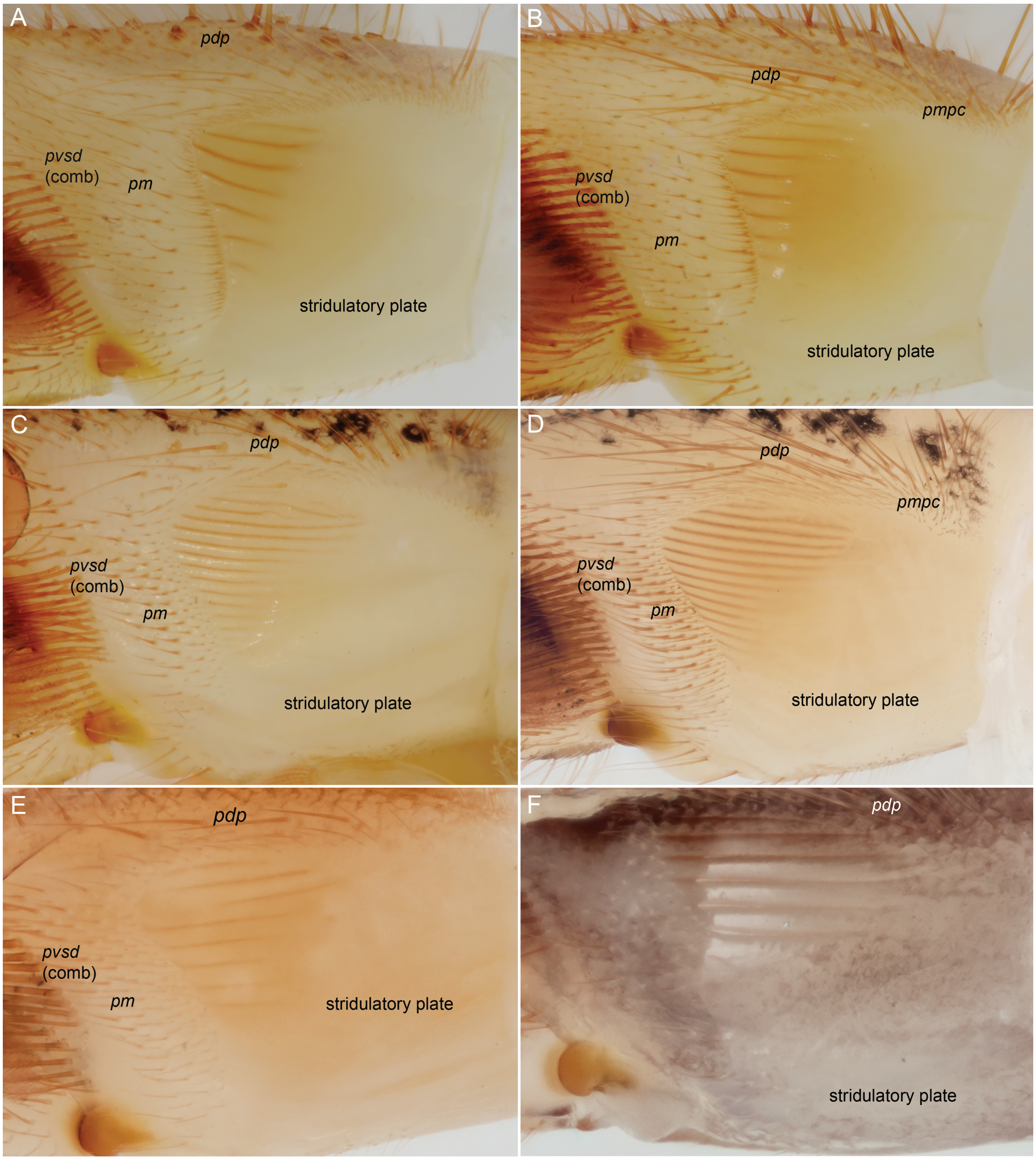

A
pdp
pvsd
(comb)
pm
stridulatory plate
B
pdp
pmpc
pvsd
(comb)
pm
stridulatory plate
C
pdp
pvsd
(comb)
pm
stridulatory plate
D
pdp
pmpc
pvsd
(comb)
pm
stridulatory plate
E
pdp
pvsd
(comb)
pm
stridulatory plate
F
pdp
stridulatory plate

PLATE 9. Solpugidae Leach, 1815 (**A, B**) and Daesiidae Kraepelin, 1899 (**C–F**), chelicerae, prolateral views, illustrating stridulatory apparatus with pronounced stridulatory ridges, field of promedial (***pm***) setae with unmodified to weakly modified stridulatory setae, prodorsal proximal (***pdp***) setae, comb of proventral subdistal (***pvsd***) setae, and setiform promedial proximal setal cluster (***pmpc***). **A, B.** *Solpugassa furcifera* (Kraepelin, 1899). **A.** ♂ (AMNH [LP 3632]). **B.** ♀ (AMNH [LP 3632]). **C, D.** *Ammotrechelis goetschi* Roewer, 1934. **C.** ♂ (AMNH [LP 10673]). **D.** ♀ (AMNH [LP 10673]). **E.** *Gluviopsilla discolor* (Kraepelin, 1899), ♂ (AMNH [LP 7516]). **F.** *Hemiblossia australis* (Purcell, 1902), ♂ (AMNH [LP 9866]).

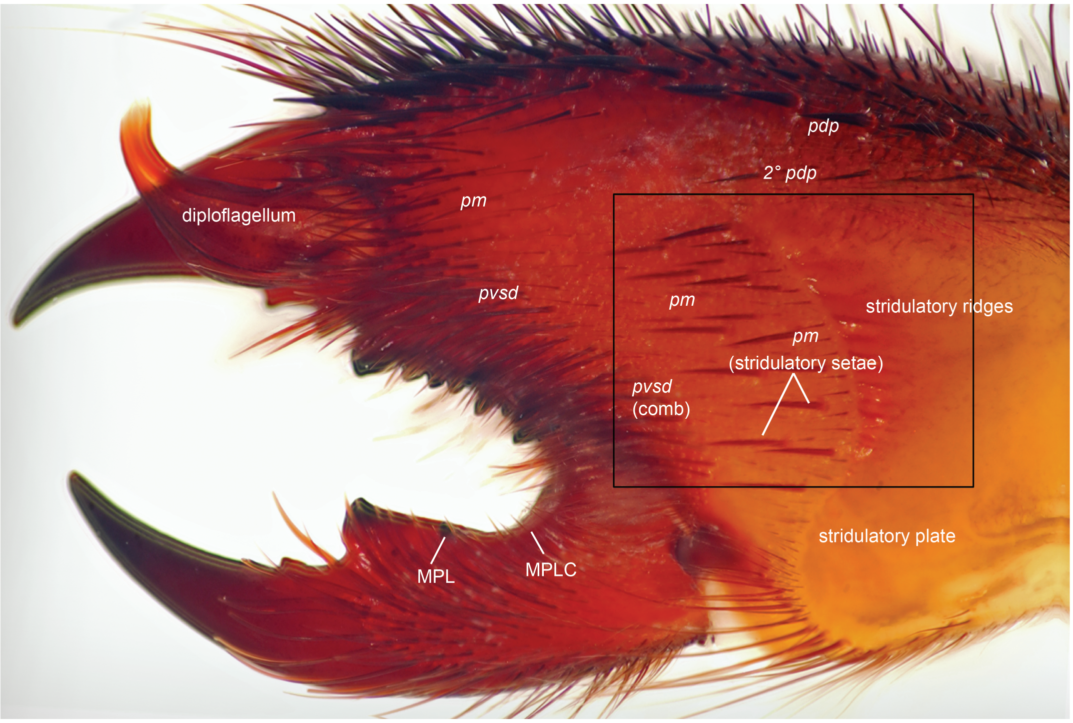

pdp
2° pdp
diploflagellum
pm
pvsd
pm
stridulatory ridges
pm
(stridulatory setae)
pvsd
(comb)
stridulatory plate
MPL
MPLC

PLATE 10. Rhagodidae Pocock, 1897, *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]), chelicera, prolateral view, illustrating stridulatory apparatus, comprising stridulatory plate, ridges and stridulatory setae (modified *pm* setae). Box illustrates approximate area depicted in plate 11. Abbreviations: **MPL,** movable finger, prolateral tooth; **MPLC,** movable finger, prolateral carina; ***pdp*,** prodorsal proximal setae; ***pm*,** promedial setae (including stridulatory setae); ***pvsd*,** proventral subdistal setae, including comb; **2°,** secondary.

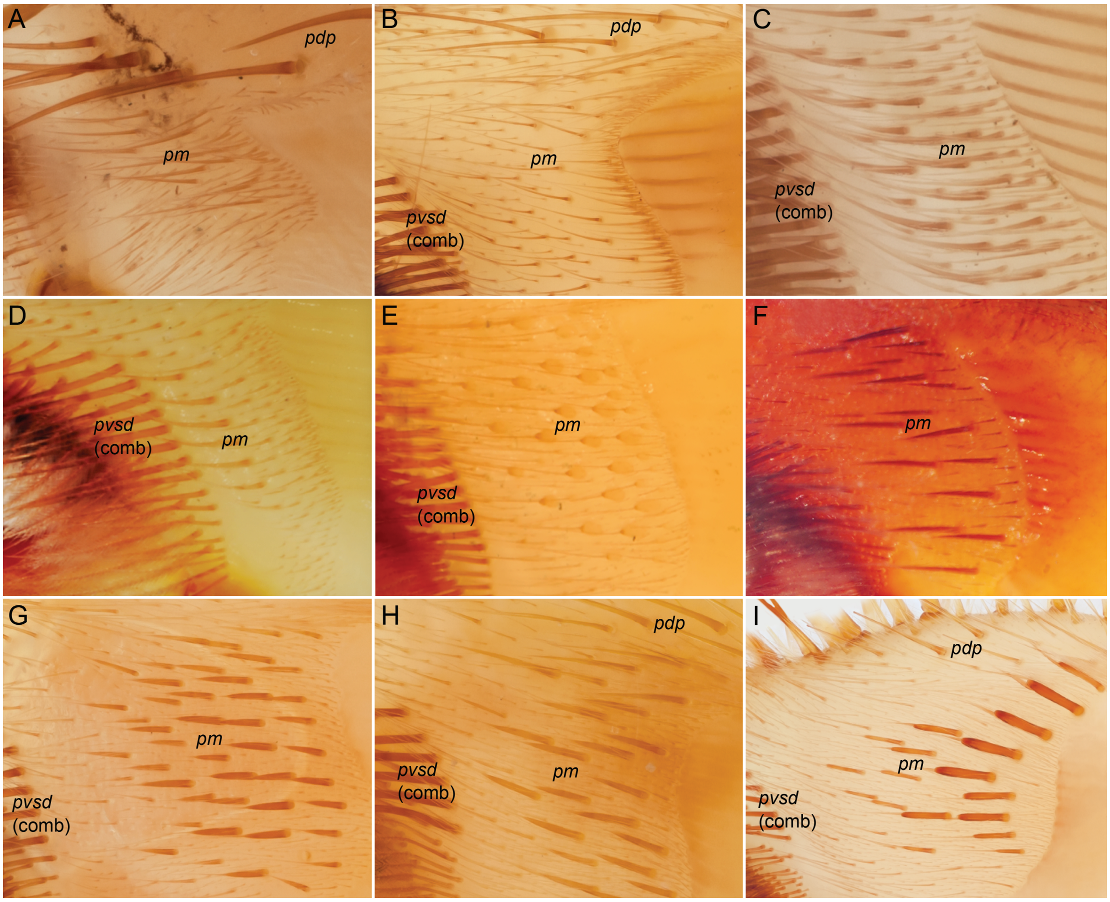

A
pdp
pm
B
pdp
pm
pvsd
(comb)
C
pm
pvsd
(comb)
D
pvsd
(comb)
pm
E
pm
pvsd
(comb)
F
pm
G
pm
pvsd
(comb)
H
pdp
pvsd
(comb)
pm
I
pdp
pm
pvsd
(comb)

PLATE 11. Karschiidae Kraepelin, 1899 (**A**), Solpugidae Leach, 1815 (**B**), Daesiidae Kraepelin, 1899 (**C**), Lipophaginae Wharton, 1981 (**D**), Eremobatidae Kraepelin, 1899 (**E**), Rhagodidae Pocock, 1897 (**F**), and Galeodidae Sundevall, 1833 (**G–I**), chelicerae, prolateral views, illustrating differentiation in stridulatory setae (modified *pm* setae). **A.** *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **B.** *Zeria lawrencei* (Roewer, 1933), ♂ (NMNW 13820). **C.** *Ammotrechelis goetschi* Roewer, 1934, ♀ (AMNH [LP 10673]). **D.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]). **E.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]). **F.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). **G.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 7536]), type II (*araneoides* type) setae. **H.** *Paragaleodes* sp., ♀ (AMNH [LP 10550]), type II (*araneoides* type) setae. **I.** *Galeodes* sp., ♂ (AMNH [LP 11204]), type I (*arabs* type) setae. Abbreviations: ***pdp*,** prodorsal proximal setae; ***pm*,** promedial setae (including stridulatory setae); ***pvsd*,** proventral subdistal setae, including comb.

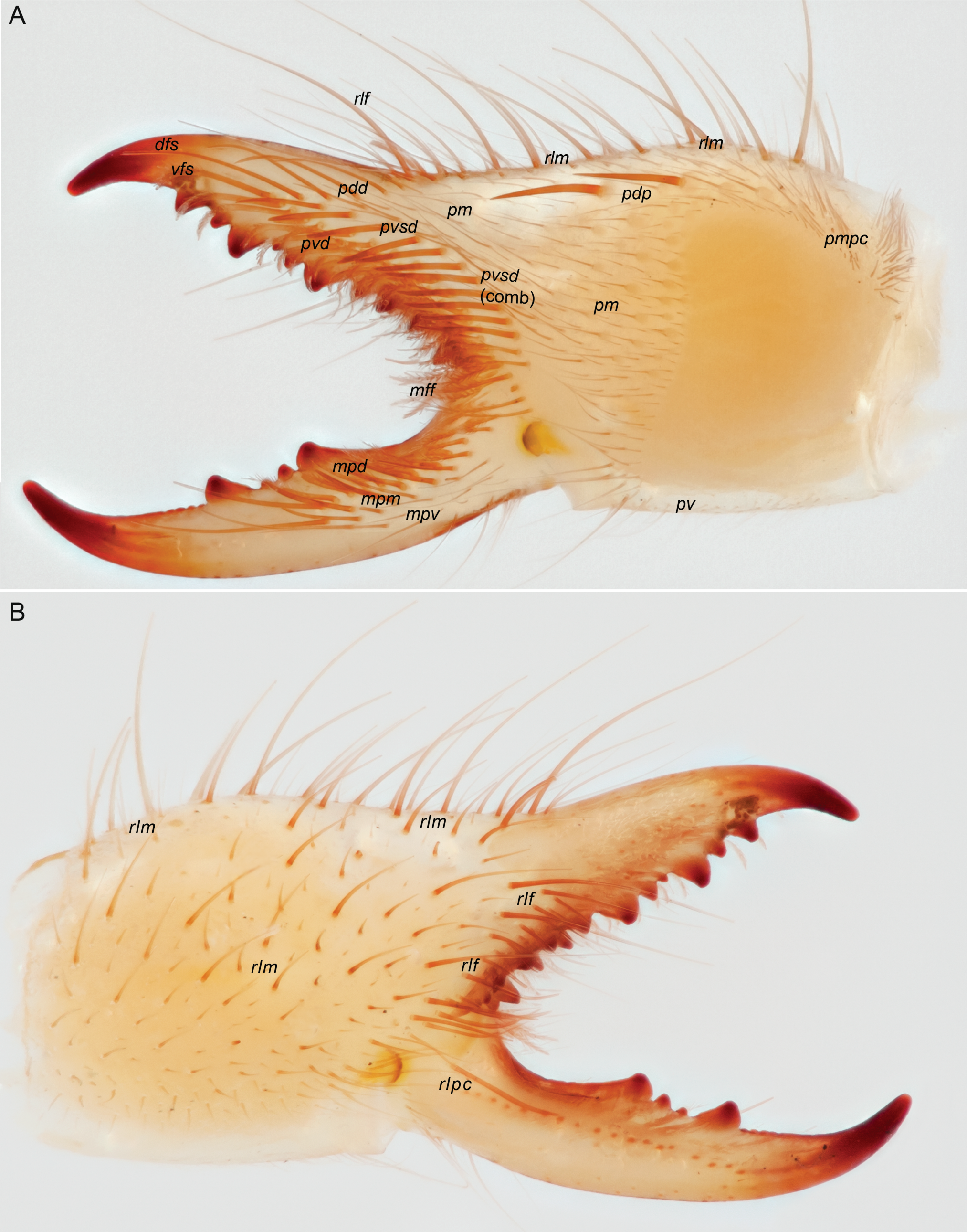

A
rlf
dfs
vfs
pdd
rlm
rlm
pdp
pm
pvsd
pvd
pvsd
(comb)
pm
pmpc
mff
mpd
mpm
mpv
pv
B
rlm
rlm
rlf
rlm
rlf
rlpc

PLATE 12. Eremobatidae Kraepelin, 1899, *Hemerotrecha branchi* Muma, 1951, ♀ (DMNS ZA.16786), chelicera, prolateral (**A**) and retrolateral (**B**) views, illustrating setal arrangements. Abbreviations: ***dfs*****,** dorsal flagellar seta; ***mff*****,** movable finger, fondal setae; ***mpd*****,** movable finger, prodorsal setae; ***mpm*****,** movable finger, promedial setae; ***mpv*****,** movable finger, proventral setae; ***pdd*****,** prodorsal distal setae; ***pdp*****,** prodorsal proximal setae; ***pm*****,** promedial setae; ***pmpc*****,** promedial proximal setal cluster; ***pv*****,** proventral setae; ***pvd*****,** proventral distal setae; ***pvsd*****,** proventral subdistal setae; ***rlf*****,** retrolateral finger setae; ***rlm*****,** retrolateral manus setae; ***rlpc*****,** retrolateral proximal setal cluster; ***vfs*****,** ventral flagellar seta.

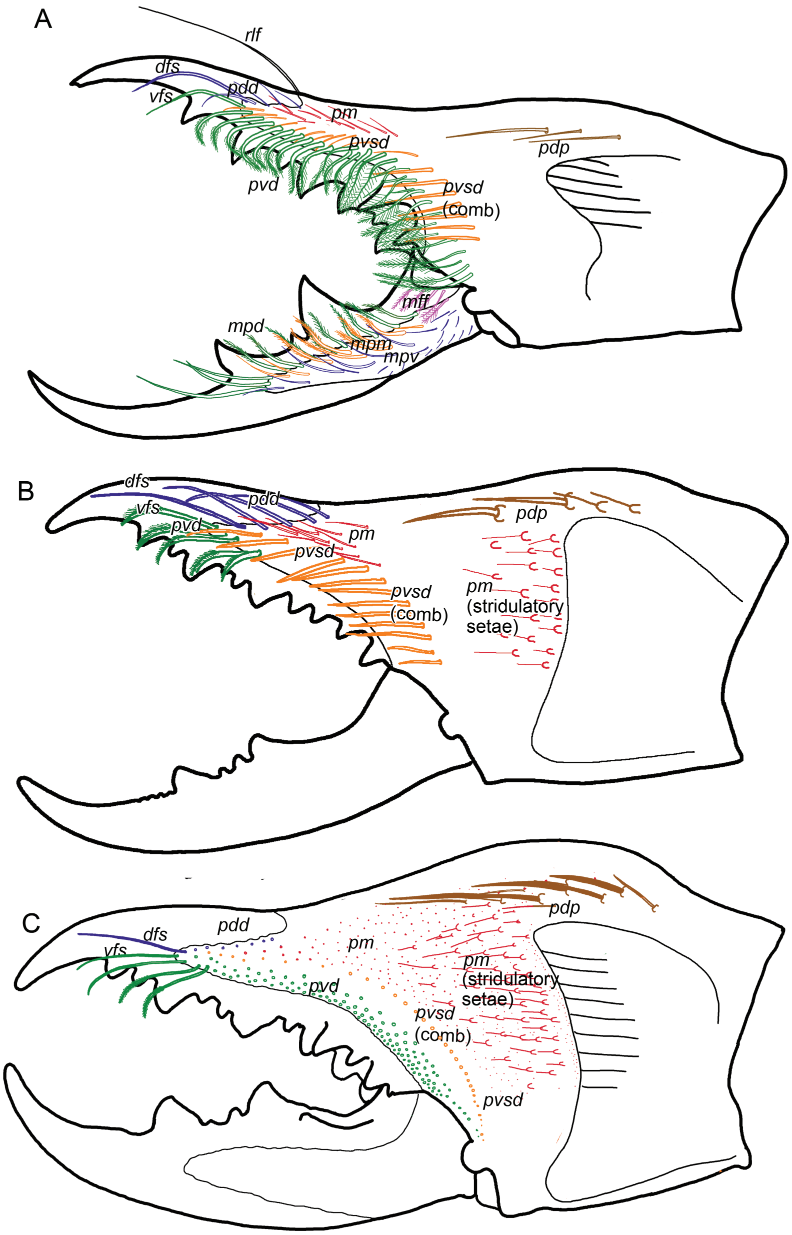

A
rlf
dfs
vfs
pdd
pm
pvsd
pvd
pvsd
(comb)
pdp
mff
mpd
mpm
mpv
B
dfs
vfs
pdd
pvd
pm
pvsd
pdp
pvsd
(comb)
pm
(stridulatory
setae)
C
dfs
vfs
pdd
pm
pdp
pvd
pm
(stridulatory
setae)
pvsd
(comb)
pvsd

PLATE 13. Solpugidae Leach, 1815 (**A**) and Eremobatidae Kraepelin, 1899 (**B, C**), chelicerae, prolateral views, illustrating setal arrangements. **A.** *Prosolpuga schultzei* (Kraepelin, 1908), ♀ (AMNH [LP 3605]). **B.** *Hemerotrecha branchi* Muma, 1951, ♂ (DMNS ZA.16786). **C.** *Eremocosta gigasella* (Muma, 1951), ♀ (DMNS ZA.17350). Selected setae indicated. Circles represent setal sockets. Abbreviations and color coding: ***dfs,*** dorsal flagellar seta; ***mff,*** movable finger, fondal setae (magenta); ***mpd,*** movable finger, prodorsal setae (green); ***mpm,*** movable finger, promedial setae (orange); ***mpv,*** movable finger, proventral setae (blue); ***pdd,*** prodorsal distal setae (blue); ***pdp,*** prodorsal proximal setae (brown); ***pm,*** promedial setae (red); ***pvd,*** proventral distal setae (green); ***pvsd,*** proventral subdistal setae (orange); ***rlf,*** retrolateral finger setae; ***vfs,*** ventral flagellar seta.

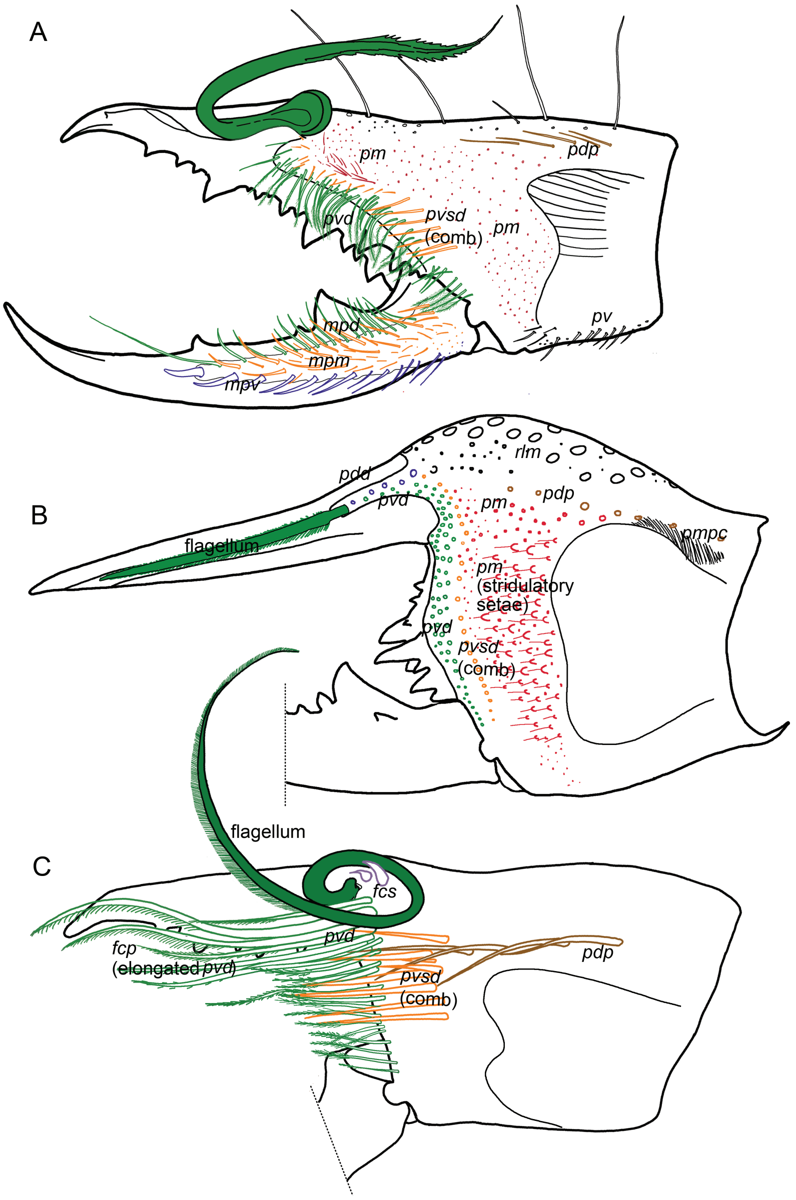

A
pm
pdp
pvd
pvsd
(comb)
pm
pv
mpd
mpm
mpv
B
pdd
rlm
pvd
pm
pdp
pmpc
flagellum
pm
(stridulatory
setae)
pvd
pvsd
(comb)
flagellum
C
fcs
fcp
(elongated pvd)
pvd
pdp
pvsd
(comb)

PLATE 14. Solpugidae Leach, 1815 (**A**), Eremobatidae Kraepelin, 1899 (**B**), and Karschiidae Kraepelin, 1899 (**C**), chelicerae, prolateral views, illustrating setal arrangements. **A.** *Solpugiba lineata* (C.L. Koch, 1842), ♂ (AMNH [LP 5919]). **B.** *Eremobates gerbae* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10000). **C.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]), illustrating elongated distal *pvd* setae (= *fcp*). Selected setae indicated in **A** and **B**. Circles represent setal sockets. Abbreviations and color coding: Flagellum colored solid green. ***fcp*,** flagellar complex plumose setae (green); ***fcs*,** flagellar complex spiniform setae (purple); ***mpd*,** movable finger, prodorsal setae (green); ***mpm*,** movable finger, promedial setae (orange); ***mpv*,** movable finger, proventral setae (blue); ***pdd*,** prodorsal distal setae (blue); ***pdp*,** prodorsal proximal setae (brown); ***pm*,** promedial setae (red); ***pmpc*,** promedial proximal setal cluster; ***pv*,** proventral setae; ***pvd*,** proventral distal setae (green); ***pvsd*,** proventral subdistal setae (orange); ***rlm*,** retrolateral manus setae.

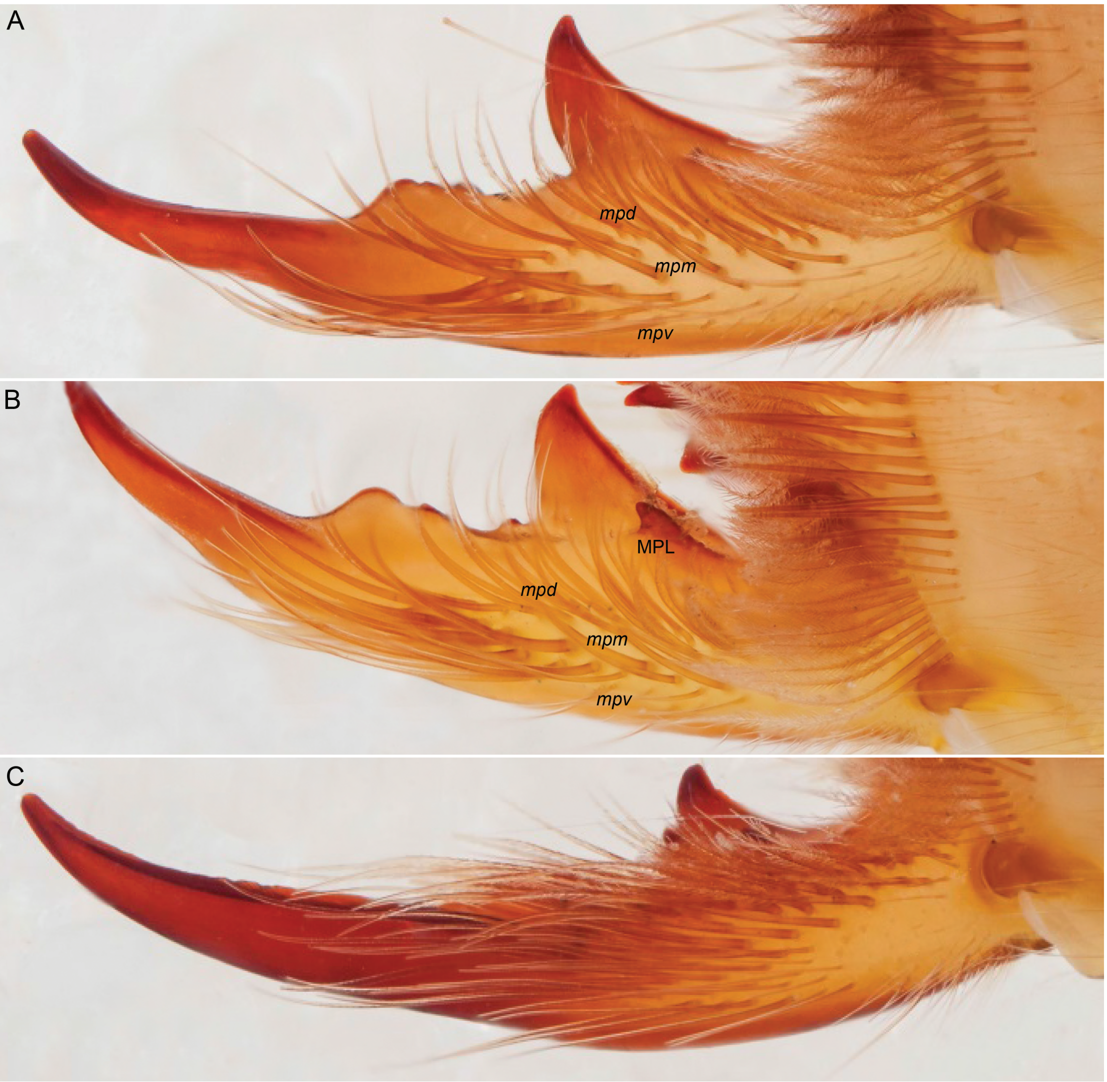


PLATE 15. Eremobatidae Kraepelin, 1899, cheliceral movable fingers, prolateral views, illustrating arrangement and differentiation of setae. **A.** *Eremobates bixleri* Muma and Brookhart, 1988, paratype ♂ (DMNS ZA.17386). **B.** *Eremobates ajoanus* Muma and Brookhart, 1988, paratype ♂ (DMNS ZA.17311). **C.** *Eremobates angustus* Muma, 1951, paratype ♂ (DMNS ZA.16788). Abbreviations: **MPL,** movable finger, prolateral tooth; ***mpd*,** movable finger, prodorsal setae; ***mpm*,** movable finger, promedial setae; ***mpv*,** movable finger, proventral setae.

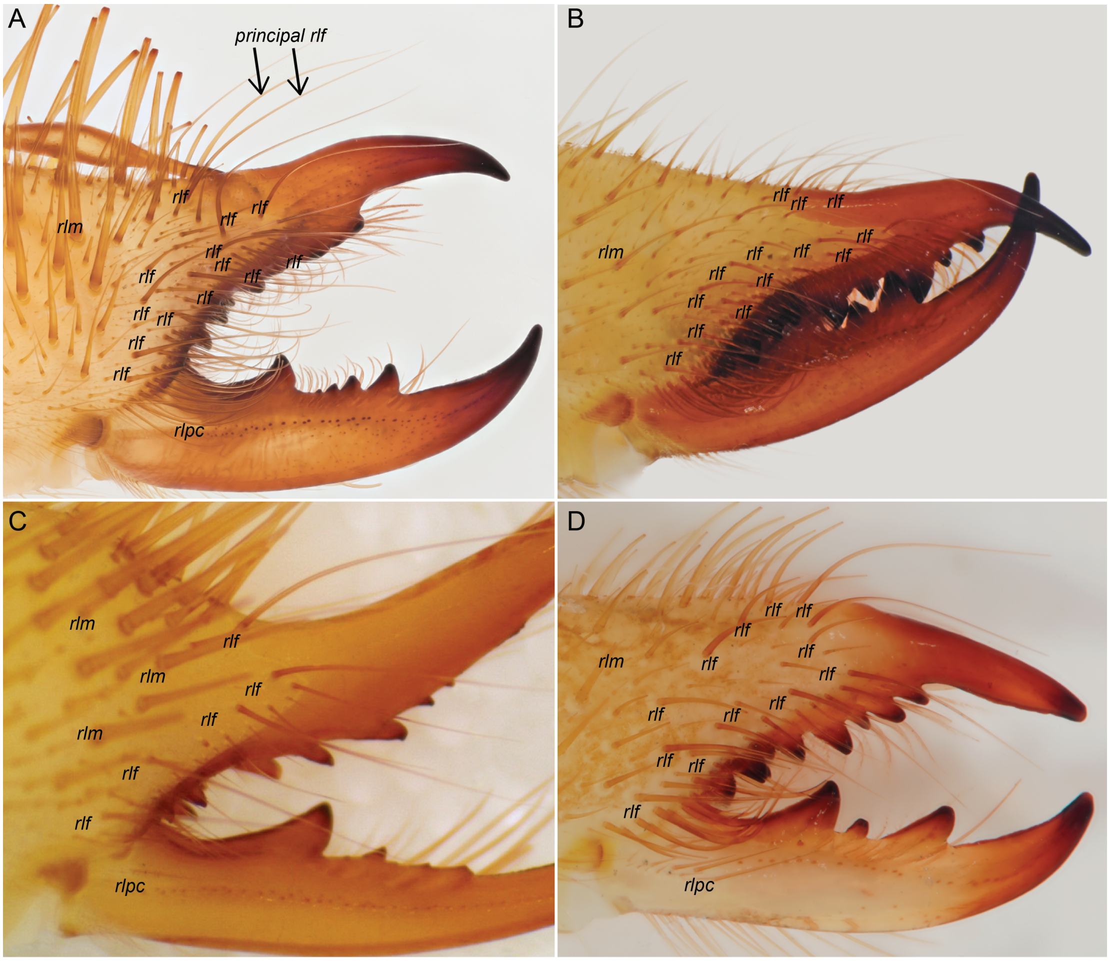

A
principal rlf
rlm
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlpc
B
rlf
rlf
rlf
rlf
rlm
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
C
rlm
rlf
rlm
rlf
rlm
rlf
rlf
rlf
rlpc
D
rlf
rlf
rlf
rlm
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlf
rlpc

PLATE 16. Galeodidae Sundevall, 1833 (**A, B**), Eremobatidae, Kraepelin, 1899 (**C**), and Ammotrechidae Roewer, 1934 (**D**), chelicerae, retrolateral views, illustrating setae. **A.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 3536]). **B.** *Galeodes olivieri* Simon, 1879, ♀ (AMNH [LP 4628]). **C.** *Chanbria regalis* Muma, 1951, ♂ (AMNH [LP 10746]). **D.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). Abbreviations: ***rlf,*** retrolateral finger setae; ***rlm,*** retrolateral manus setae; ***rlpc,*** retrolateral proximal setal cluster.

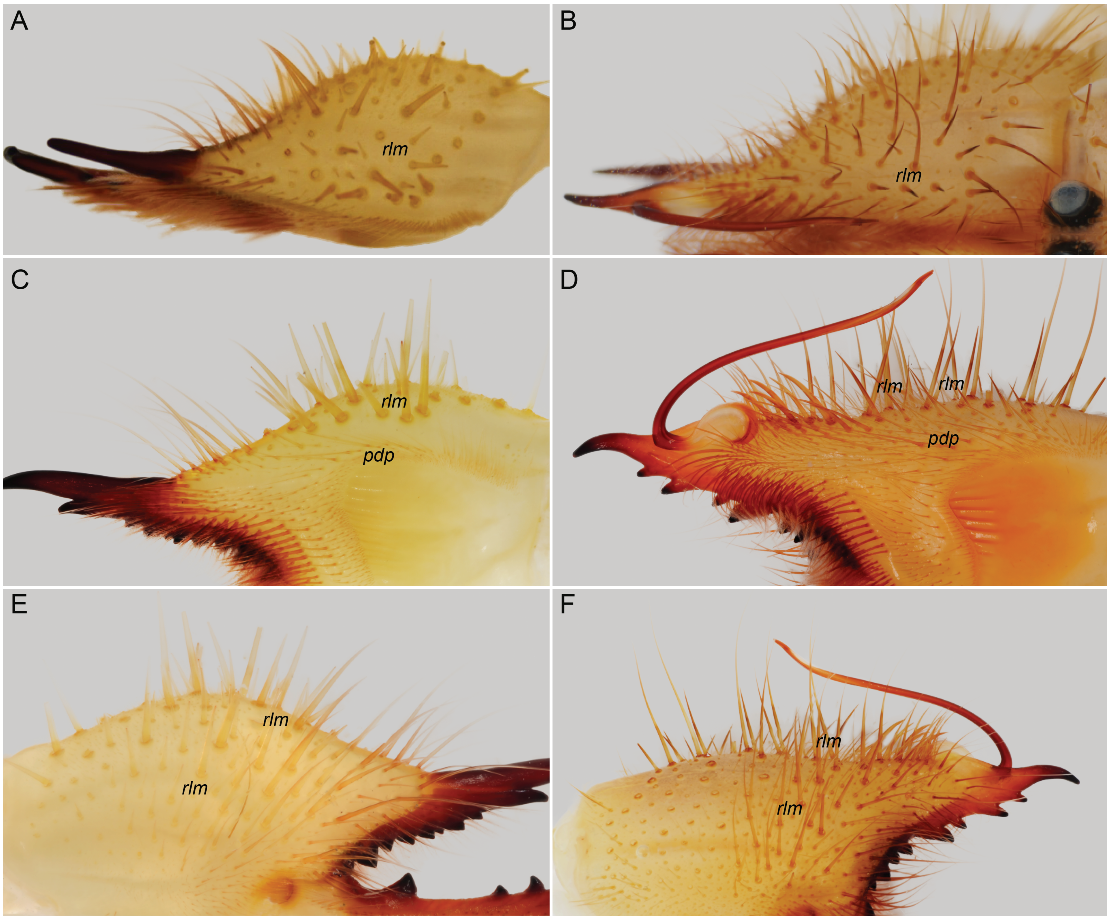


PLATE 17. Lipophaginae Wharton, 1981 (**A, C, E**) and Solpugidae Leach, 1815 (**B, D, F**), chelicerae, dorsal (**A, B**), prolateral (**C, D**) and retrolateral (**E, F**) views, illustrating dorsal setae resembling retrolateral setae, arranged in row along prodorsal edge of chelicera. **A, C, E.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]), Namibia: Namib-Naukluft Park, Garub. **B, D, F.** *Zeria lawrencei* (Roewer, 1933), ♂ (AMNH [LP 9906]). Abbreviations: ***pdp*****,** prodorsal proximal setae; ***rlm*****,** retrolateral manus setae.

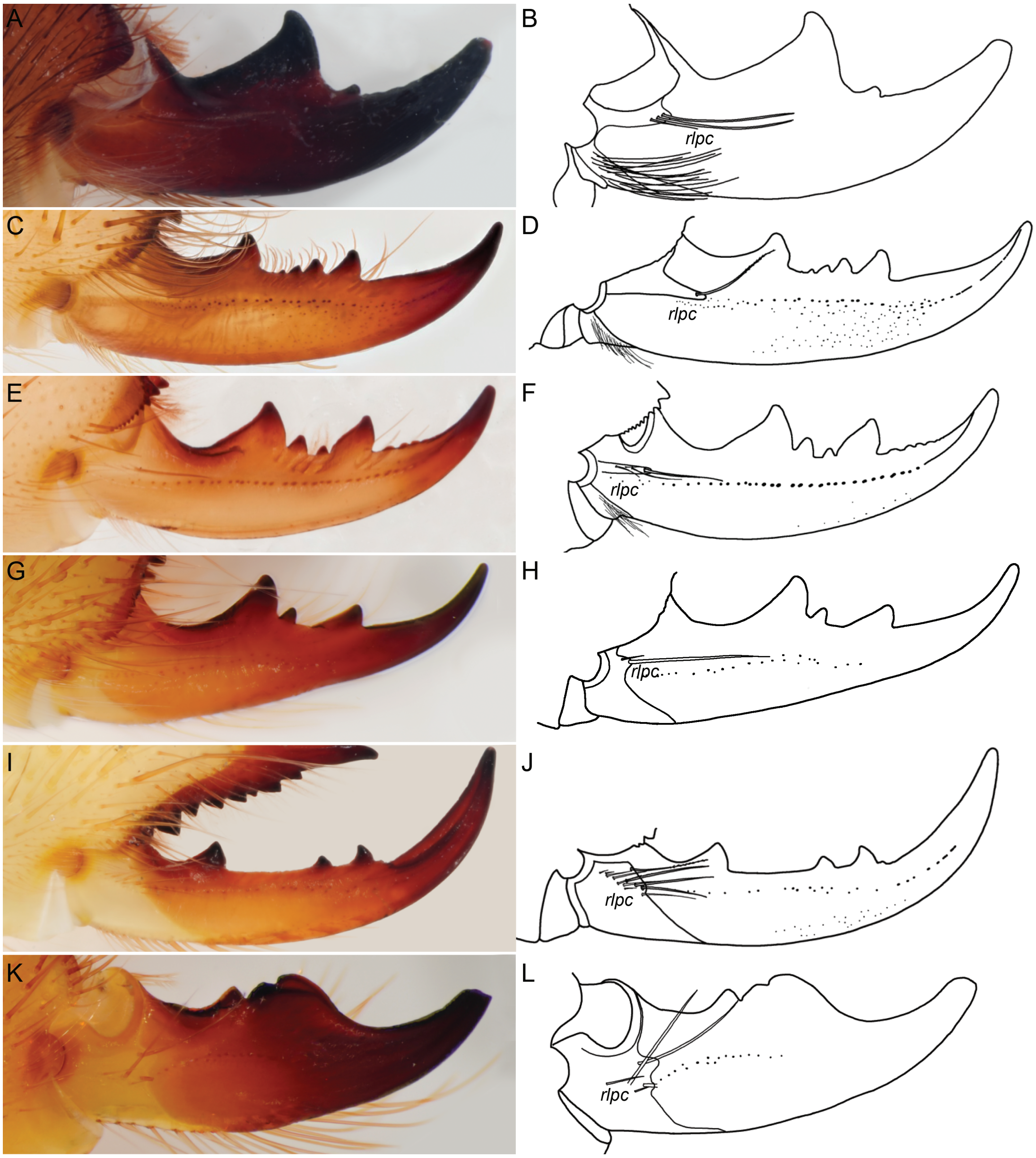


PLATE 18. Rhagodidae Pocock, 1897 (**A, B**), Galeodidae Sundevall, 1833 (**C, D**), Eremobatidae Kraepelin, 1899 (**E, F**), Gylippinae Roewer 1933 (**G, H**), Lipophaginae Wharton, 1981 (**I, J**), and Ceromidae Roewer, 1933 (**K, L**), cheliceral movable fingers, retrolateral views, illustrating retrolateral proximal setal cluster (***rlpc***) and asetose area. **A, B.** *Rhagodes melanus* (Olivier, 1807), ♂ (AMNH [LP 2293]). **C, D.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 7536]). **E, F.** *Eremobates corpink* Brookhart and Cushing, 2004, paratype ♀ (DMNS ZA.17379). **G, H.** *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **I, J.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]). **K, L.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106).

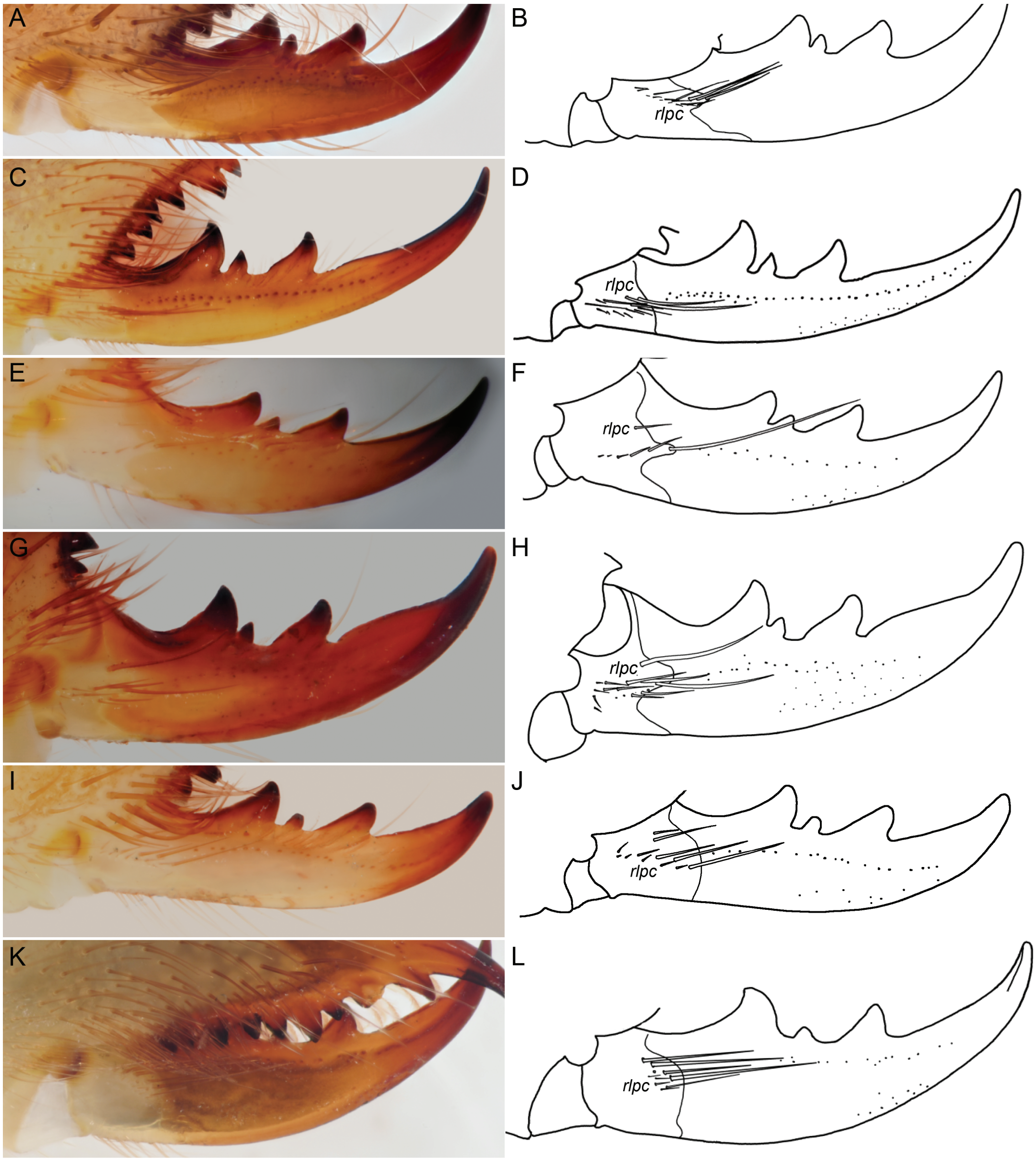


PLATE 19. Solpugidae Leach, 1815 (**A, B**), Daesiidae Kraepelin, 1899 (**C–H**), Ammotrechidae Roewer, 1934 (**I, J**), and Mummuciidae Roewer, 1934 (**K, L**), cheliceral movable fingers, retrolateral views, illustrating retrolateral proximal setal cluster (***rlpc***) and asetose area. **A, B.** *Solpugyla* sp., ♀ (AMNH [LP 10764]). **C, D.** *Namibesia pallida* Lawrence, 1962, ♀ (AMNH [LP 4017]). **E, F.** *Blossia grandicornis* Lawrence, 1929, ♂ (AMNH [LP 5905]). **G, H.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **I, J.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **K, L.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]).

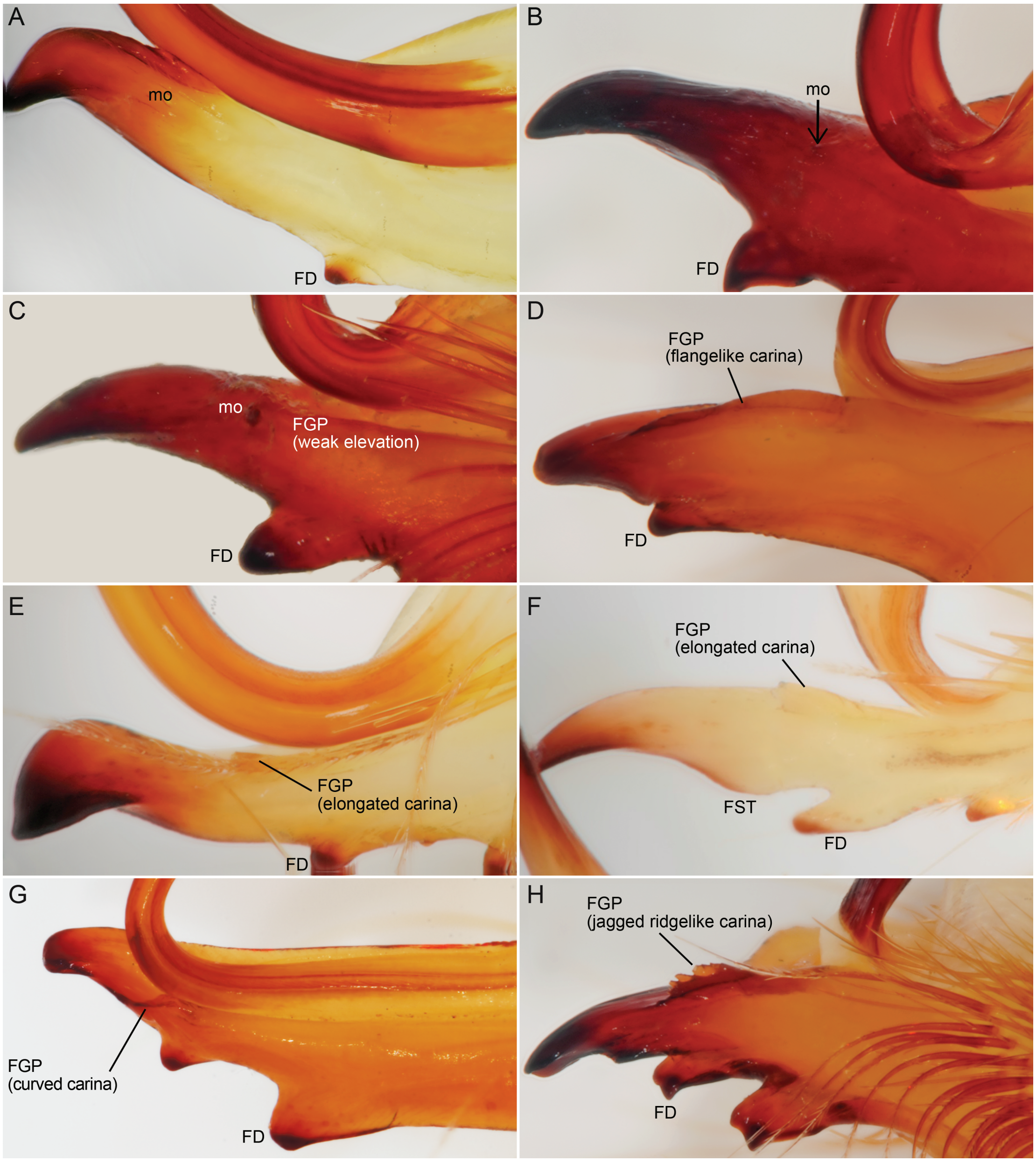

A
mo
FD
B
mo
FD
C
mo
FGP
(weak elevation)
FD
D
FGP
(flangelike carina)
FD
E
FGP
(elongated carina)
FD
F
FGP
(elongated carina)
FST
FD
G
FGP
(curved carina)
FD
H
FGP
(jagged ridgelike carina)
FD

PLATE 20. Solpugidae Leach, 1815, cheliceral fixed finger mucra, prolateral views, indicating mucron organ (mo) and different manifestations of flagellar groove process (FGP). **A.** *Metasolpuga picta* (Kraepelin, 1899), ♂ (AMNH [LP 10719]). **B.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **C.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]). **D.** *Solpuga chelicornis* Lichtenstein, 1796, ♂ (AMNH [LP 8158]). **E.** *Solpugista bicolor* (Lawrence, 1953), ♂ (AMNH [LP 7933]). **F.** *Solpugema genucornis* (Lawrence, 1935), ♂ (AMNH [LP 8167]). **G.** *Solpugema hamata* (Hewitt, 1914), ♂ (TMSA 6632). **H.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). Abbreviations: **FD,** fixed finger, distal tooth; **FGP,** flagellar groove process; **FST,** fixed finger, subterminal flange; **mo,** mucron organ.

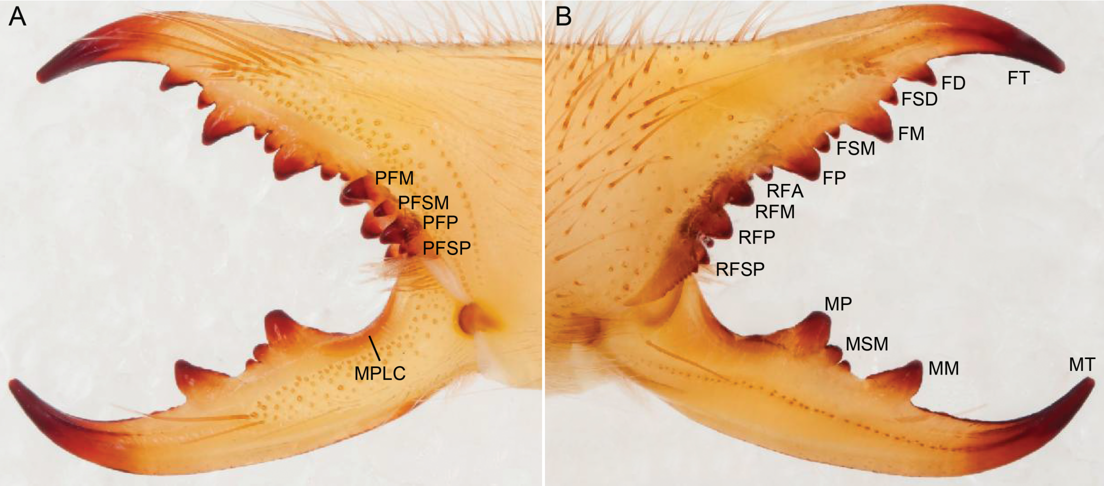
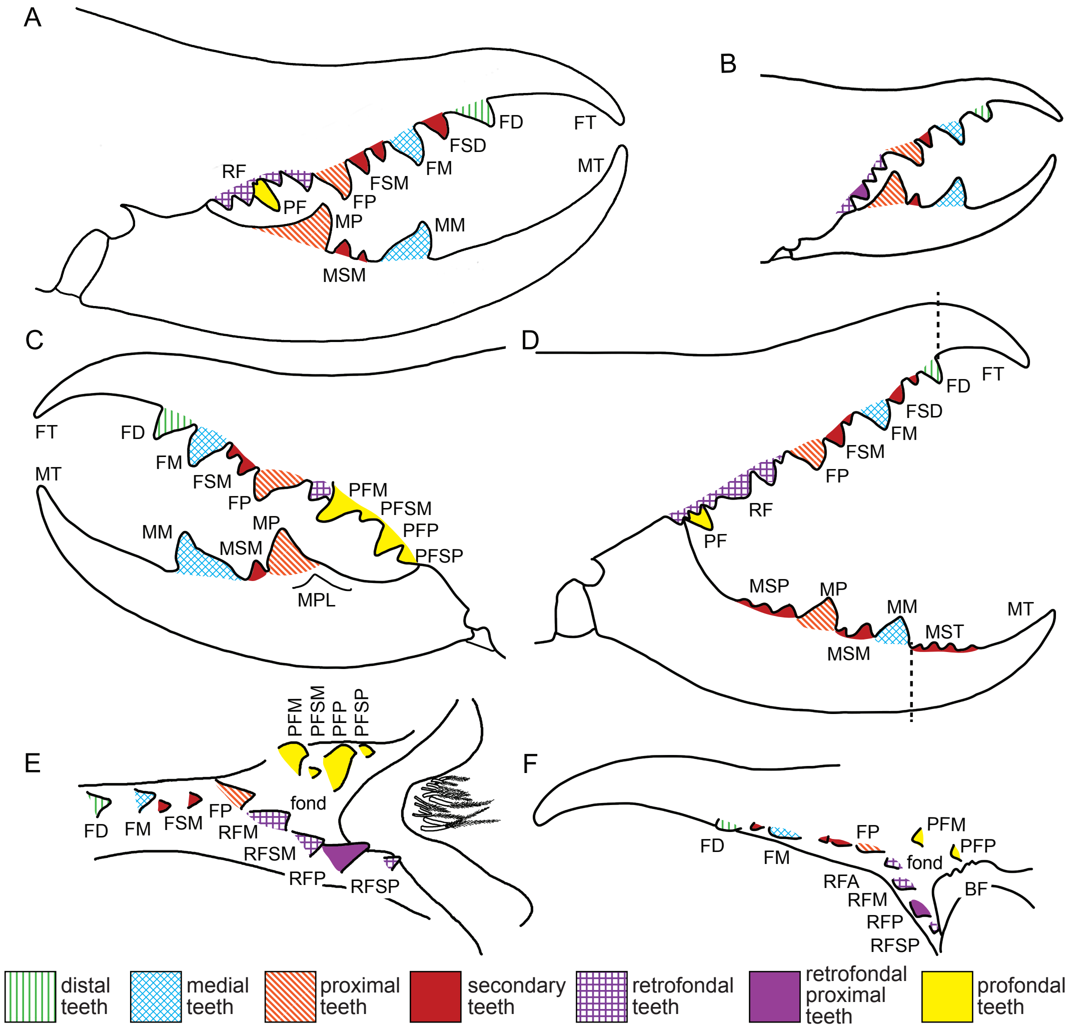


PLATE 21. Eremobatidae Kraepelin, 1899, *Eremobates polhemusi* Muma and Brookhart, 1988, ♀ (DMNS ZA.10004), chelicera, prolateral (**A**) and retrolateral (**B**) views, indicating primary, secondary and fondal teeth. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **FT,** fixed finger, terminal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPLC,** movable finger, prolateral carina; **MSM,** movable finger, submedial teeth; **MT,** movable finger, terminal tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth.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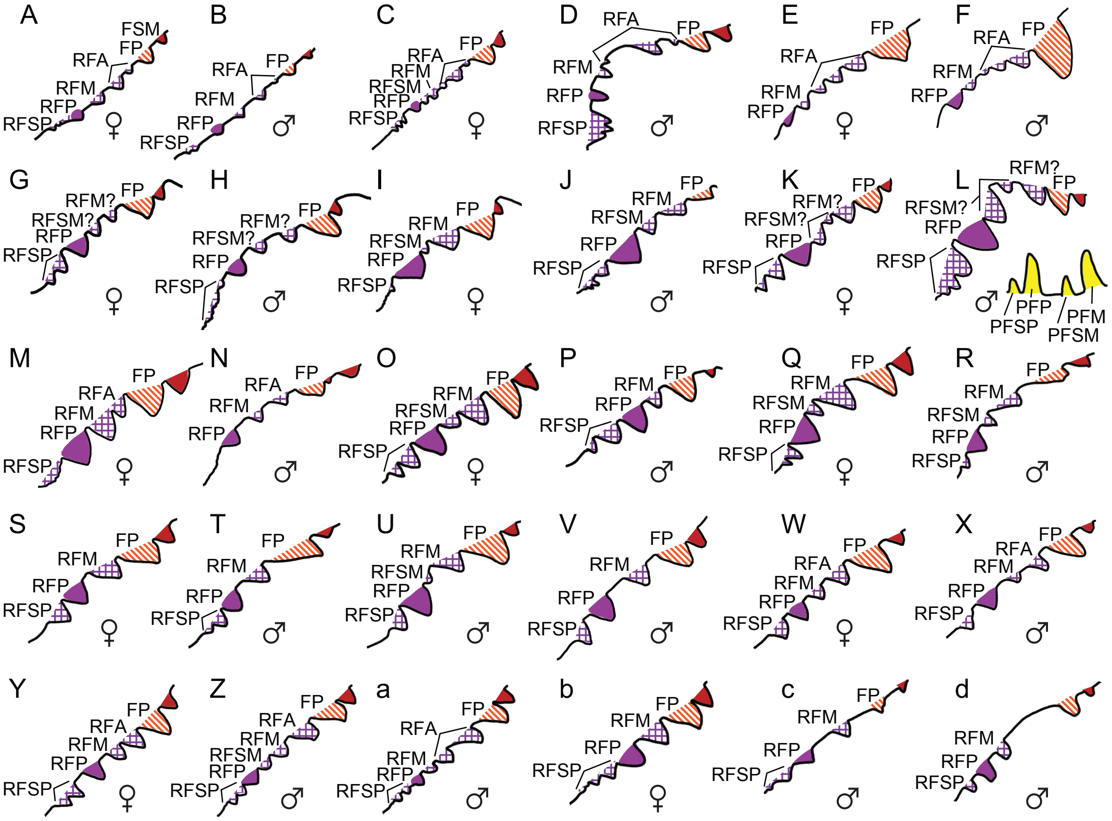
FM
FP
PFM
PFP
fond
RFA
RFM
BF
RFP
RFSP
distal teeth
medial teeth
proximal teeth
secondary teeth
retrofondal teeth
retrofondal proximal teeth
profondal teeth

PLATE 22. Ammotrechidae Roewer, 1934 (**A**), Solpugidae Leach, 1815 (**B, C, E**), Karschiidae Kraepelin, 1899 (**D**), and Galeodidae Sundevall, 1833 (**F**), chelicerae, retrolateral (**A, B, D**) and prolateral (**C**) views, and fixed finger ventral (**E**) and proventral (**F**) views, indicating terminological abbreviations and color coding for dentition applied elsewhere. **A.** *Sedna pirata* Muma, 1971, ♀ (AMNH [LP 2362]). **B.** *Zeria lawrencei* (Roewer, 1933), ♀ (NMNW 13820), illustrating typical conserved or putatively plesiomorphic dentition pattern. **C.** *Solpugassa furcifera* (Kraepelin, 1899), ♀ (AMNH [LP 3632]). **D.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **E.** *Zeria sericea* (Pocock, 1897), ♂ (NMNW 13801). **F.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]). Mucra indicated distal to dotted lines (**A, D**). Abbreviations: **BF,** basifondal teeth; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth/teeth; **FSM,** fixed finger, submedial tooth/teeth; **FT,** fixed finger, terminal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MSM,** movable finger, submedial tooth/teeth; **MSP,** movable finger, subproximal tooth/teeth; **MST,** movable finger, subterminal teeth; **MT,** movable finger, terminal tooth; **PF,** profondal teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **RF,** retrofondal teeth; **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal.


A
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RFA
RFM
RFSM
RFP
RFSP
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D
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FP
RFM
RFP
RFSP
♂
E
FP
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F
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G
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RFM?
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RFSP
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FP
RFM?
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K
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RFSP
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L
RFM?
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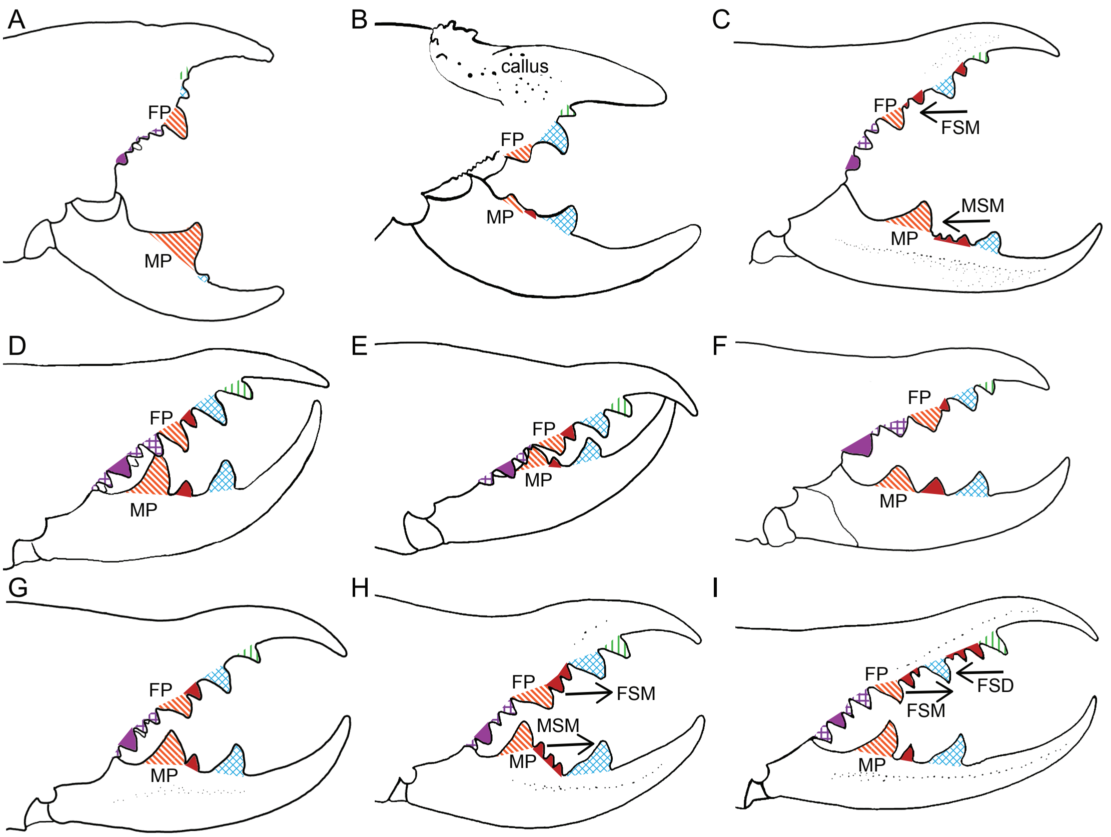
a
FP
RFA
RFM
RFP
RFSP
♂
b
FP
RFM
RFP
RFSP
♀
c
FP
RFM
RFP
RFSP
♂
d
RFM
RFP
RFSP
♂

PLATE 23. Karschiidae Kraepelin, 1899 (**A–D**), Rhagodidae, Pocock, 1897 (**E, F**), Gylippinae Roewer, 1933 (**G, H**), Lipophaginae Wharton, 1981 (**I–L**), Galeodidae Sundevall, 1833 (**M, N**), Ceromidae Roewer, 1933 (**O, P**), Solpugidae Leach, 1815 (**Q, R**), Daesiidae Kraepelin, 1899 (**S–V**), Ammotrechidae Roewer, 1934 (**W, X**), Mummuciidae Roewer, 1934 (**Y–a**), Melanoblossiinae Roewer, 1933 (**b, c**) and Dinorhaxinae Roewer, 1933 (**d**), retrofondal teeth, retrolateral views, except profondal teeth (yellow) prolateral view (**L**). **A, B.** *Eusimonia divina* Birula, 1935, ♀ (AMNH [LP 4098]) (**A**), ♂ (AMNH [LP 4098]) (**B**). **C, D.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♀ (AMNH [LP 7476]) (**C**), ♂ (AMNH [LP 7474]) (**D**). **E, F.** *Rhagodes melanus* (Olivier, 1807), ♀ (AMNH [LP 10549]) (**E**), ♂ (AMNH [LP 2293]) (**F**). **G.** *Gylippus* (*Anoplogylippus*) *ferganensis* Birula, 1893, juv. (AMNH [LP 3921]). **H.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **I, J.** *Trichotoma michaelseni* (Kraepelin, 1914), ♀ (NMNW 12757) (**I**), ♂ (AMNH [LP 5724]) (**J**). **K, L.** *Bdellophaga angulata* Wharton, 1981, ♀ (NMNW 12240) (**K**), ♂ (NMNW 11601) (**L**). **M.** *Paragaleodes* sp., ♀ (AMNH [LP 10550]). **N.** *Paragaleodes nesterovi* Birula, 1916, ♂ (AMNH [LP 7480]). **O, P.** *Ceroma inerme* Purcell, 1899, ♀ (AMNH [LP 8425]) (**O**), ♂ (AMNH [LP 9864]) (**P**). **Q, R.** *Oparba asiatica* (Turk, 1948), ♀ (TAUZM 50313) (**Q**), ♂ (HUJI 360) (**R**). **S, T.** *Blossia grandicornis* Lawrence, 1929, ♀ (AMNH [LP 5905]) (**S**), ♂ (AMNH [LP 5905]) (**T**). **U.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **V.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **W, X.** *Pseudocleobis andinus* (Pocock, 1899), ♀ (AMNH [LP 2384]) (**W**), ♂ (AMNH [LP 2384]) (**X**). **Y, Z.** *Gaucha fasciata* Mello-Leitão, 1924, ♀ (AMNH [LP 5858]) (small RFSM tooth absent on sinistral chelicera) (**Y**), ♂ (AMNH [LP 10699]) (**Z**). **a.** *Uspallata* cf. *pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). **b, c.** *Melanoblossia braunsi*, Purcell, 1903, ♀ (AMNH [LP 10737]) (**b**), ♂ (AMNH [LP 10737]) (**c**). **d.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). Abbreviations: **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **RFA,** retrofondal apical tooth/teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth/teeth; **RFSP,** retrofondal subproximal tooth/teeth.


A
FP
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FP
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C
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FSM
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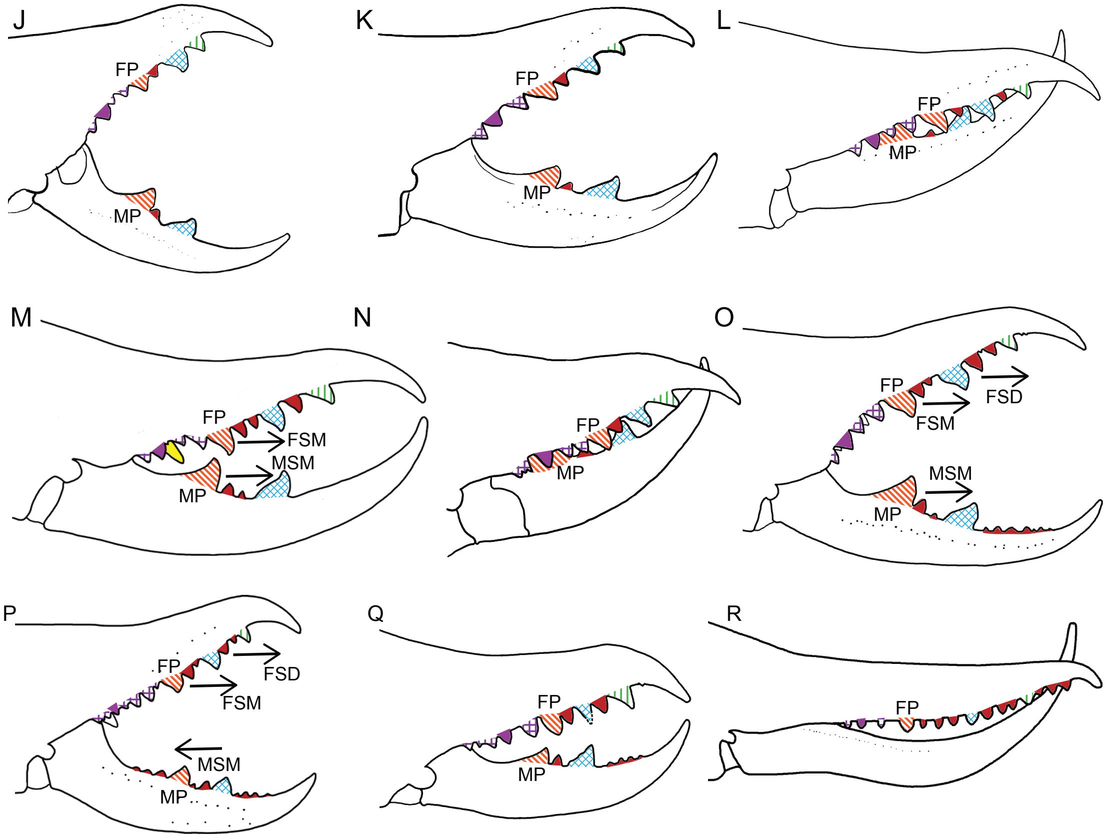
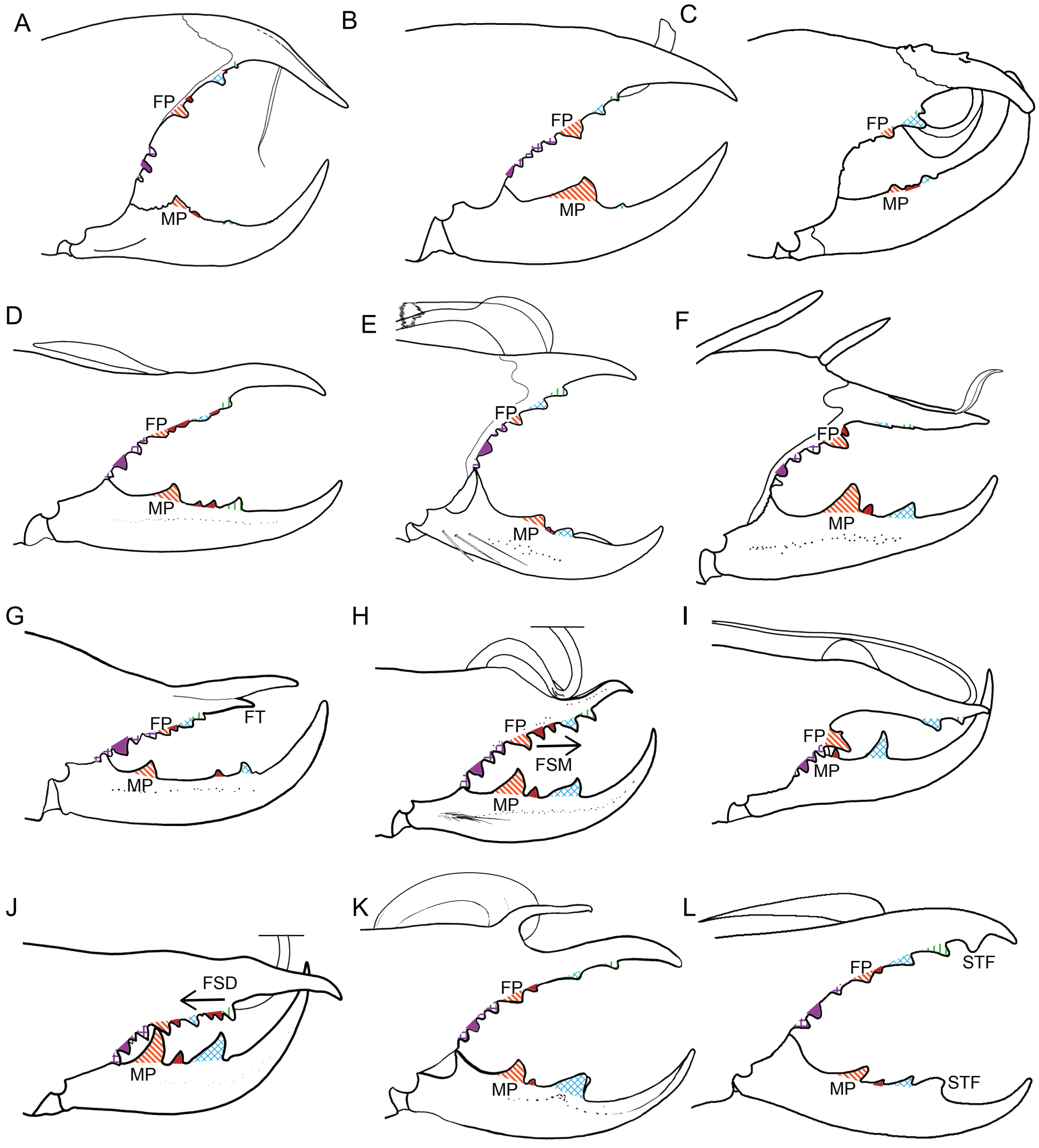


PLATE 24. Rhagodidae, Pocock, 1897 (**A**), Hexisopodidae Pocock, 1897 (**B**), Galeodidae Sundevall, 1833 (**C**), Ceromidae Roewer, 1933 (**D**), Gylippinae Roewer, 1933 (**E**), Lipophaginae Wharton, 1981 (**F**), Solpugidae Leach, 1815 (**G, H**), Daesiidae Kraepelin, 1899 (**I–K**), including Namibesiinae Wharton, 1981 (**I**), Ammotrechidae Roewer, 1934 (**L, M**), Mummuciiae Roewer, 1934 (**N**), Eremobatidae Kraepelin, 1899 (**O**), Karschiidae Kraepelin, 1899 (**P**), and Melanoblossiinae Roewer, 1933 (**Q, R**), female chelicerae, retrolateral views, summarizing typical dentition patterns. **A.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **A.** *Rhagodes melanus* (Olivier, 1807), ♂ (AMNH [LP 2293]). **B.** *Hexisopus aureopilosus* Lawrence, 1968, ♀ (NMNW 11203). **C.** *Galeodes araneoides* (Pallas, 1772), ♀ (AMNH), Turkey: Gurgen. **D.** *Ceroma inerme* Purcell, 1899, ♀ (AMNH [LP 8425]). **E.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♀ (KUT), Turkey: Kayseri Province. **F.** *Trichotoma michaelseni* (Kraepelin, 1914), ♀ (NMNW 12757). **G.** *Solpuga chelicornis* Lichtenstein, 1796, ♀ (NCA 2008/3524). **H.** *Zeria fusca* (C.L. Koch, 1842), ♀ (AMNH [LP 1472]). **I.** *Namibesia pallida* Lawrence, 1962, ♀ (AMNH [LP 4017]). **J.** *Ammotrechelis goetschi* Roewer, 1934, ♀ (AMNH [LP 10673]). **K.** *Blossia grandicornis* Lawrence, 1929, ♀ (AMNH [LP 5905]). **L.** *Pseudocleobis andinus* (Pocock, 1899), ♀ (AMNH [LP 2384]). **M.** *Sedna pirata* Muma, 1971, ♀ (AMNH [LP 2362]). **N.** *Gaucha fasciata* Mello-Leitão, 1924, ♀ (AMNH [LP 10699]). **O.** *Horribates bantai* Muma, 1989, ♀ (DMNS ZA.17691). **P.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **Q.** *Melanoblossia braunsi* Purcell, 1903, ♂ (AMNH [LP 10737]). **R.** *Lawrencega minuta* Wharton, 1981, paratype ♂ (CAS 9033898). Arrows indicate secondary teeth size-gradation patterns. Abbreviations: **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth.


A
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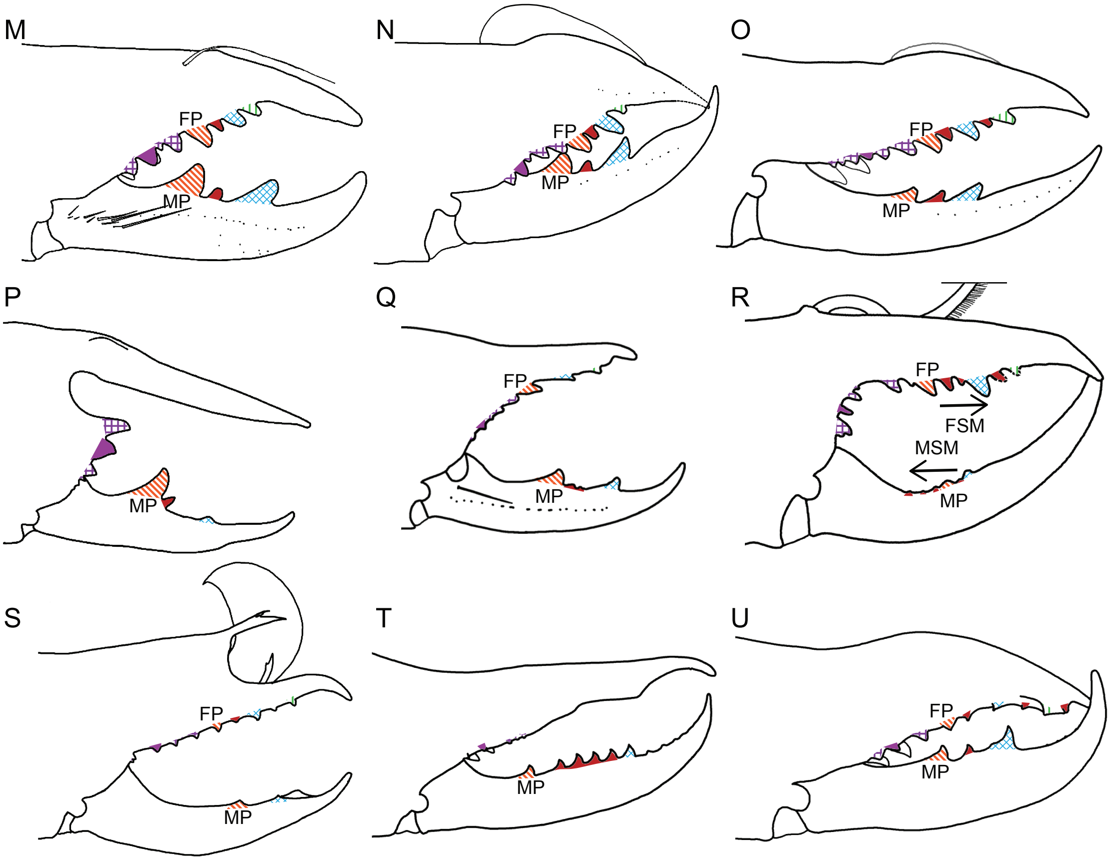
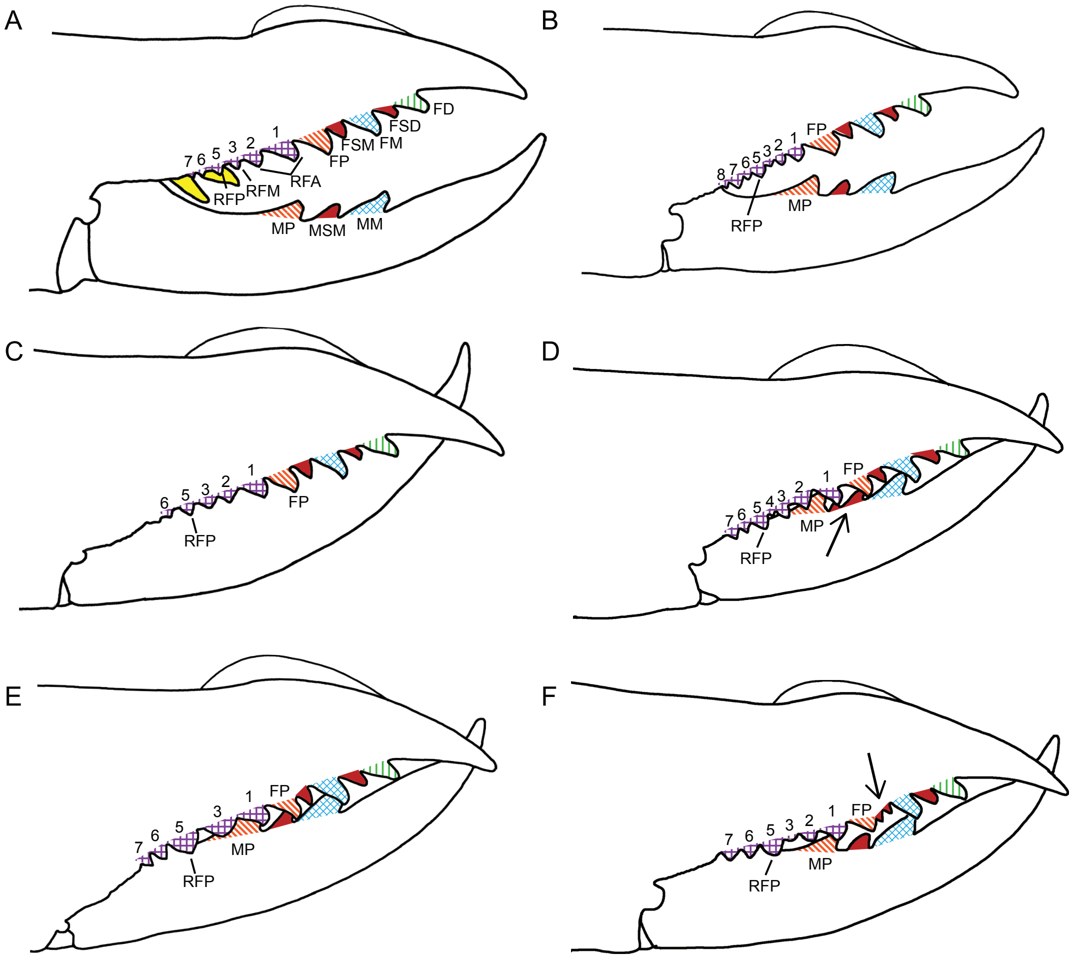


PLATE 25. Dinorhaxinae Roewer, 1933 (**A**) Rhagodidae Pocock, 1897 (**B**), Hexisopodidae Pocock, 1897 (**C**), Galeodidae Sundevall, 1833 (**D**), Ceromidae Roewer, 1933 (**E**), Gylippinae Roewer, 1933 (**F**), Lipophaginae Wharton, 1981 (**G**), Solpugidae Leach, 1815 (**H, I**), Daesiidae Kraepelin, 1899 (**J–L**), including Namibesiinae Wharton, 1981 (**J**), Ammotrechidae Roewer, 1934 (**M**), Mummuciidae Roewer, 1934 (**N, O**), Eremobatidae Kraepelin, 1899 (**P, Q**), and Karschiidae Kraepelin, 1899 (**R, S**), and Melanoblossiinae (**T, U**), male chelicerae, retrolateral views, summarizing typical dentition patterns. **A.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **B.** *Rhagodes melanus* (Olivier, 1807), ♂ (AMNH [LP 2293]). **C.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **D.** *Galeodes araneoides* (Pallas, 1772), ♂ (AMNH), Turkey: Gurgen. **E.** *Ceromella* sp., ♂ (AMNH [LP 8527]). **F.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **G.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (NMNW 5724). **H.** *Solpugassa furcifera* (Kraepelin, 1899), ♂ (AMNH [LP 3632]). **I.** *Solpugema derbiana* (Pocock, 1895), ♂ (AMNH [LP 7709]). **J.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]). **K.** *Ammotrechelis goetschi* Roewer, 1934, ♂ (AMNH [LP 10673]). **L.** *Blossia* cf. *rooica* (NMNW), Namibia: Gondwana Cañon Park. **M.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **N.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]). **O.** *Uspallata* cf. *pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). **P.** *Eremobates bajadae* Muma and Brookhart, 1988, ♂ (AMNH [LP 5740]). **Q.** *Hemerotrecha branchi* Muma, 1951, ♂ (DMNS ZA.16786). **R.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]). **S.** *Eusimonia divina* Birula, 1935, ♂ (AMNH [LP 4098]), **T.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). **U.** *Melanoblossia braunsi* Purcell, 1903, ♂ (AMNH [LP 10737]). Arrows indicate secondary teeth size-gradation patterns. Abbreviations: **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **FT,** fixed finger, terminal tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **STF,** subterminal flange.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MP
RFP

PLATE 26 Mummuciidae Roewer, 1934, chelicerae, retrolateral views (**A–F**), illustrating variation in closure and dentition (arrows) among individuals from a single population. **A–F.** *Uspallata* cf. *pulchra* Mello-Leitão, 1938, 5♂ (AMNH [LP 2403]). **A, B, E.** 3♂, dextral chelicerae. **C, D.** ♂, sinistral (**C**) and dextral (**D**) chelicerae. **F.** ♂, sinistral chelicera. Numbers indicate possible homologs (RFA: 1, 2; RFM: 3; RFSM: 4; RFP: 5; RFSP: 6, 7, 8). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth/teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth/teeth; **RFA,** retrofondal apical tooth/teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth/teeth. Sinistral chelicerae are illustrated in mirror image for ease of comparison.

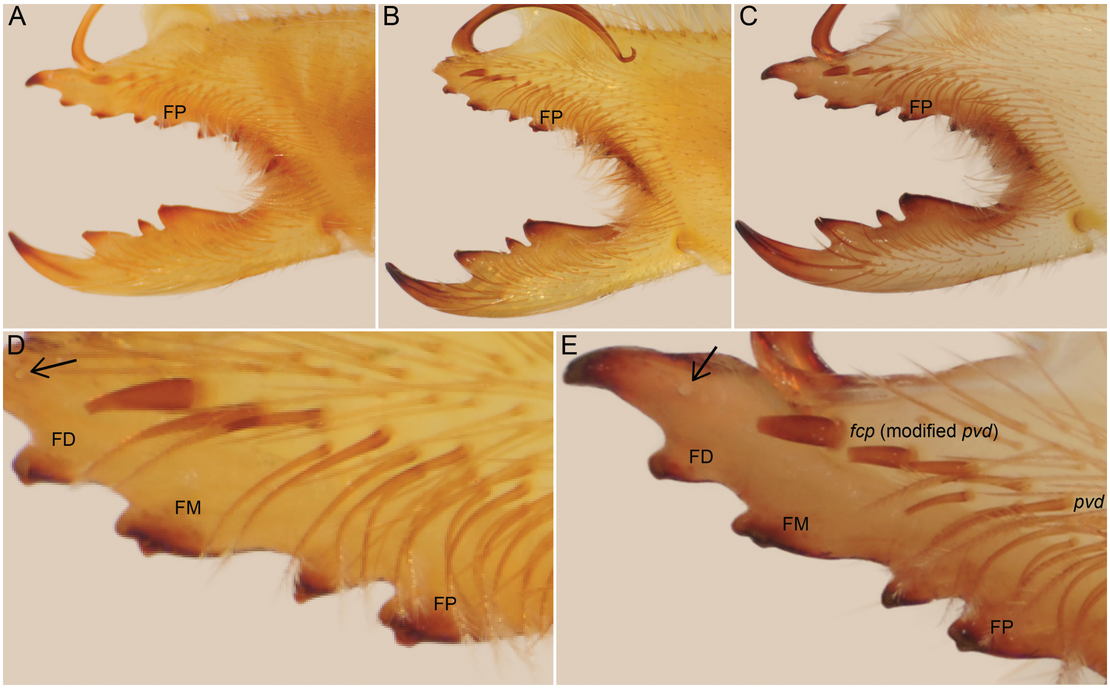


PLATE 27. Solpugidae Leach, 1815, *Oparba asiatica* (Turk, 1948), chelicerae (**A–C**) and fixed fingers (**D, E**), prolateral views, indicating interpopulation similarity in pattern of dentition and shape of primary teeth. **A.** Holotype ♂ (HUJI). **B, D.** ♂ (HUJI 360), distal half of fixed finger mucron broken. **C, E.** ♂ (HUJI 684). Arrows indicate mucron organ (mo). Abbreviations: ***fcp*,** flagellar complex plumose setae; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; ***pvd*,** proventral distal setae.

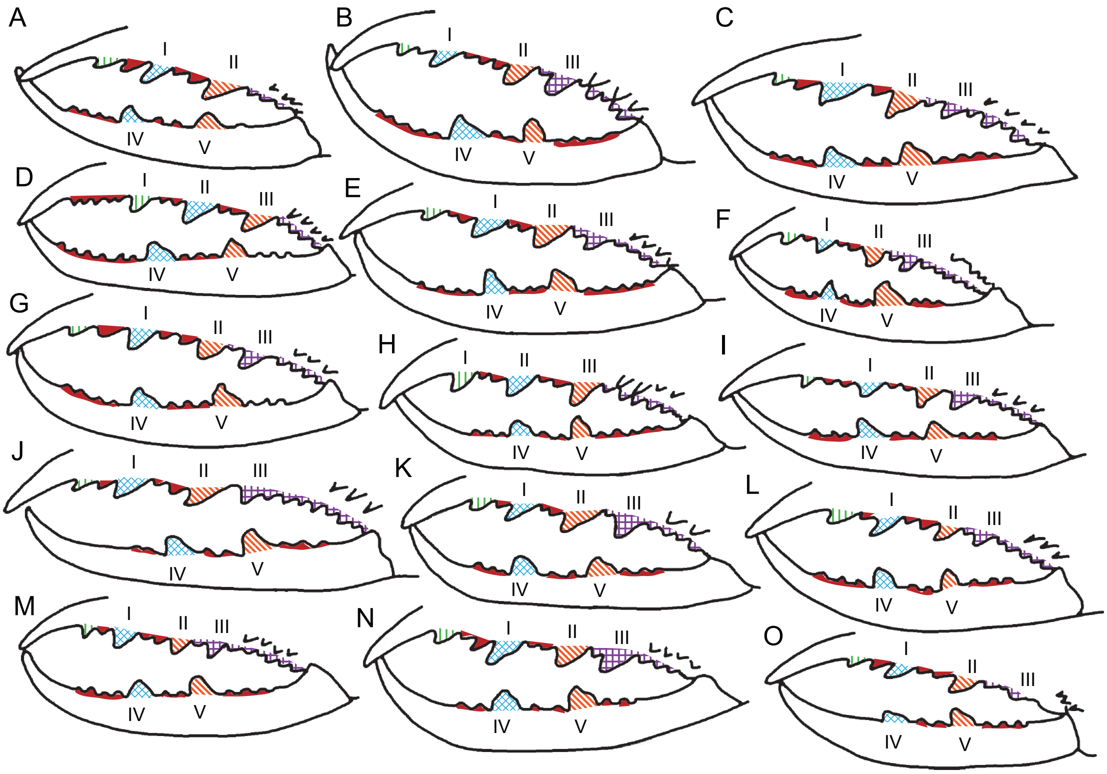


PLATE 28. Karschiidae Kraepelin, 1899, *Karschia* Walter, 1889 (**A–D, J–L, N, O**), and *Eusimonia* Kraepelin, 1899 (**E–I, M**), chelicerae, prolateral views, reproduced and adapted from Roewer (1934: 296, fig. 223), indicating his interpretation of female dentition in Roman numerals and interpretation presented here, color coded. **A.** *Karschia* (*Rhinokarschia*) *pedaschenkoi* Birula, 1922, **B.** *K.* (*K.*) *tarimina* Roewer, 1933. **C.** *K.* (*K.*) *tienschanica* Roewer, 1933. **D.** *K.* (*K.*) *mongolica* Roewer, 1933. **E.** *E. arabica* Roewer, 1933. **F.** *E. furcillata* (Simon, 1872). **G.** *E. seistanica* Roewer, 1933. **H.** *E. nigrescens* Kraepelin, 1899. **I.** *E. kabiliana* (Simon, 1879). **J.** *K.* (*K.*) *mastigofera* Birula, 1890. **K.** *K.* (*K.*) *persica* Kraepelin, 1899. **L.** *K.* (*R.*) *rhinoceros* Birula, 1922. **M.** *Barella birulae* Roewer, 1933, currently in synonymy with *E. turkestana* Kraepelin, 1899. **N.** *K.* (*K.*) *tibetana* Hirst, 1907. **O.** *K.* (*R.*) *kaznakovi* Birula, 1922. Abbreviations, annotations and color coding: Roewer's (1934) interpretation indicated with Roman numerals (I, II, III, IV); interpretation presented here indicated with color and patterns. **FD,** fixed finger, distal tooth (I, green); **FM,** fixed finger, medial tooth (II, blue); **FP,** fixed finger, proximal tooth (III, red pattern); **MM,** movable finger, medial tooth (IV, blue); **MP,** movable finger, proximal tooth (V, red pattern); secondary teeth (solid red).

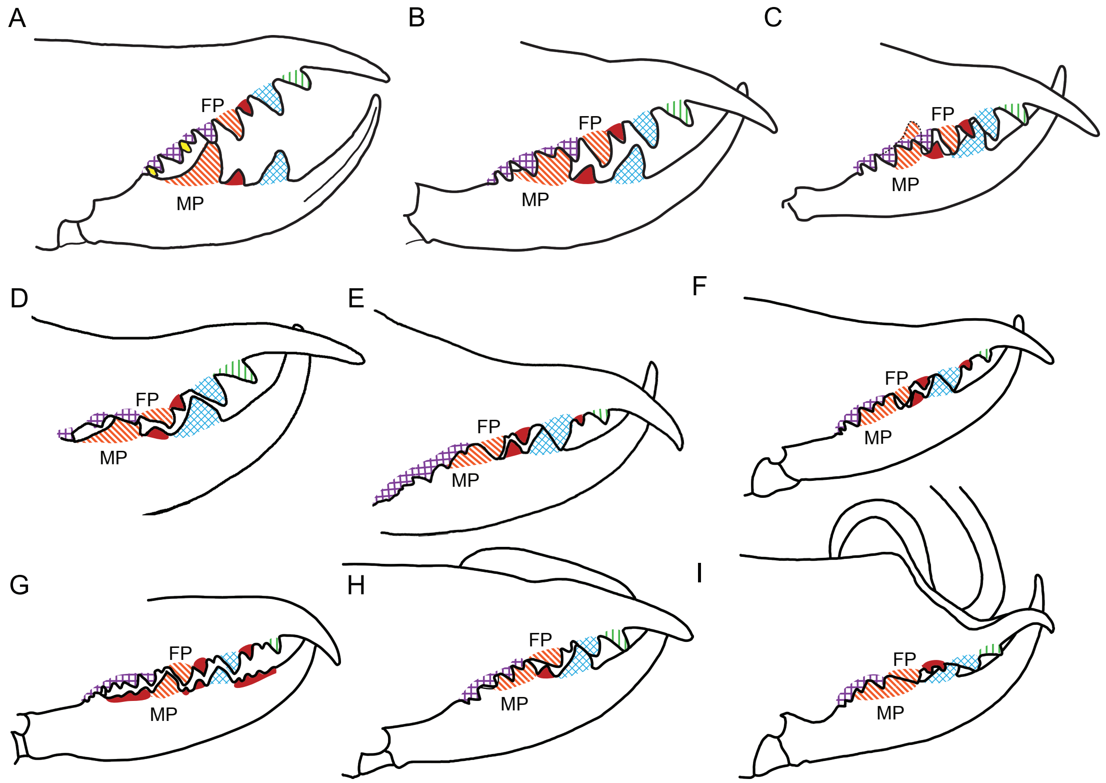


PLATE 29. Ceromidae Roewer, 1933 (**A–C**), Galeodidae Sundevall, 1833 (**D–F**), Karschiidae Kraepelin, 1899 (**G**), Ammotrechidae Roewer, 1934 (**H**), and Solpugidae Leach, 1815 (**I**), chelicerae, retrolateral views, indicating manner of closure of fixed (dorsal) versus movable (ventral) finger dentition (homology criterion 3) from relatively conserved (**A–F, H**) to highly modified (**G, I**) dentition patterns. **A–C.** *Ceroma inerme* Purcell, 1899. ♀ (AMNH [LP 8425]). **D, E.** *Galeodes* sp. ♀ (MCZ), Niger: Birni N'kare. **F.** *Galeodes olivieri* Simon 1879, ♀ (AMNH [LP 4628]). **G.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **H.** *Ammotrecha stollii* (Pocock, 1895), ♂ (AMNH [LP 8605]). **I.** *Zeria fusca* (C.L. Koch, 1842), ♂ (AMNH [LP 1473]). Abbreviations: **FP,** fixed finger, proximal tooth; **MP,** movable finger, proximal tooth.

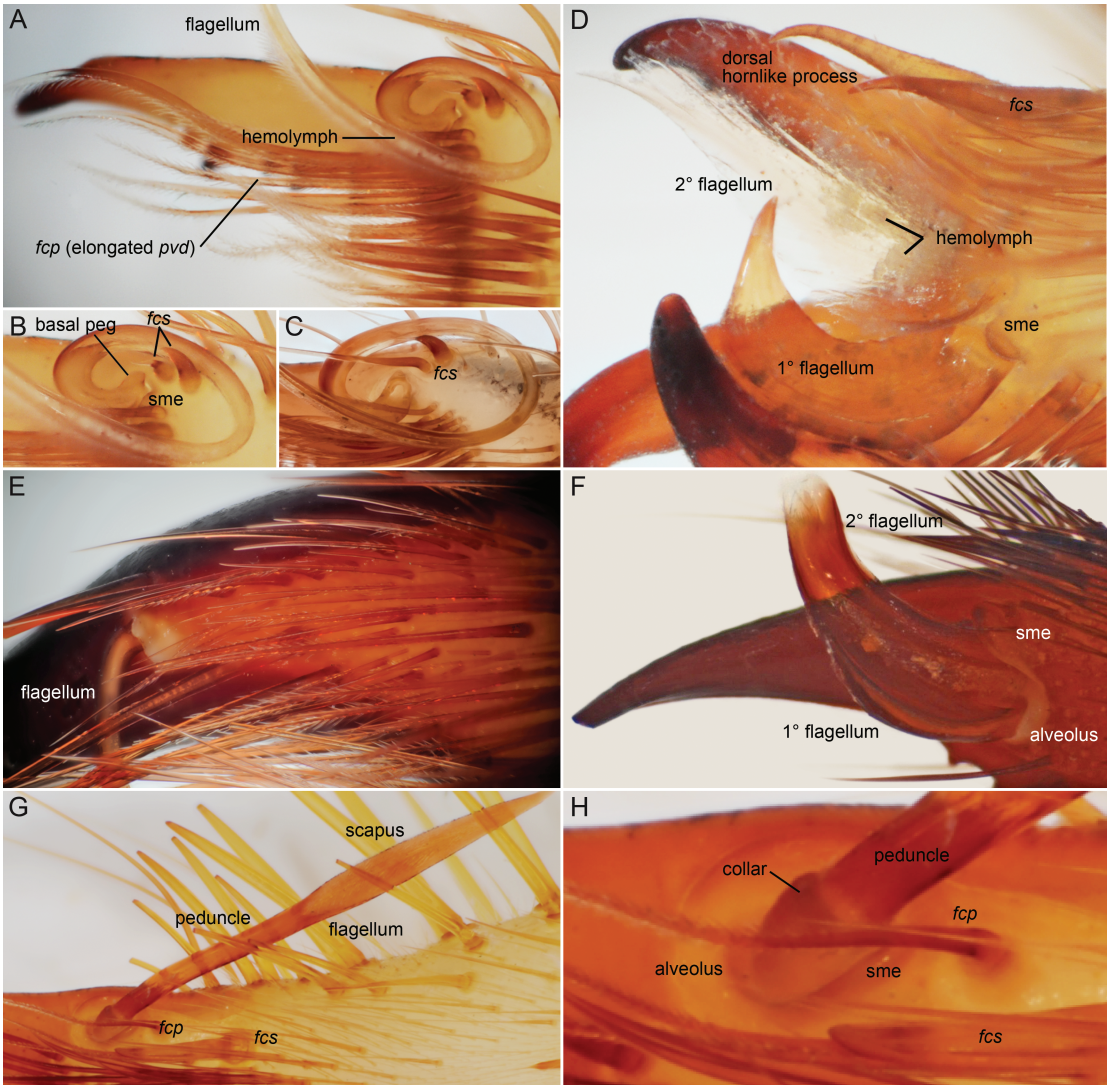

A
flagellum
hemolymph
fcp (elongated pvd)
B
basal peg
fcs
sme
C
fcs
D
dorsal
hornlike process
fcs
2° flagellum
hemolymph
sme
1° flagellum
E
flagellum
F
2° flagellum
sme
1° flagellum
alveolus
G
scapus
peduncle
flagellum
fcp
fcs
H
peduncle
collar
fcp
alveolus
sme
fcs

PLATE 30. Karschiidae Kraepelin, 1899 (**A–D**), Dinorhaxinae Roewer, 1933 (**E**), Rhagodidae, Pocock, 1897 (**F**), and Galeodidae Sundevall, 1833 (**G, H**), male flagellar complex comprising sessile flagella and associated setae, prolateral views. **A, B.** *Karschia (K.) mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]). **C.** *Karschia (K.) tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **D.** *Eusimonia nigrescens* Kraepelin, 1899, ♂ (AMNH [LP 7473]). **E.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **F.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW 14226). **G, H.** *Galeodes olivieri* Simon 1879, ♂ (AMNH [LP 4630]). Abbreviations: ***fcp*****,** flagellar complex plumose setae; ***fcs*****,** flagellar complex subspiniform to spiniform setae; ***pvd*****,** proventral distal setae; **sme,** socket margin elevation; **1°,** primary; **2°,** secondary.

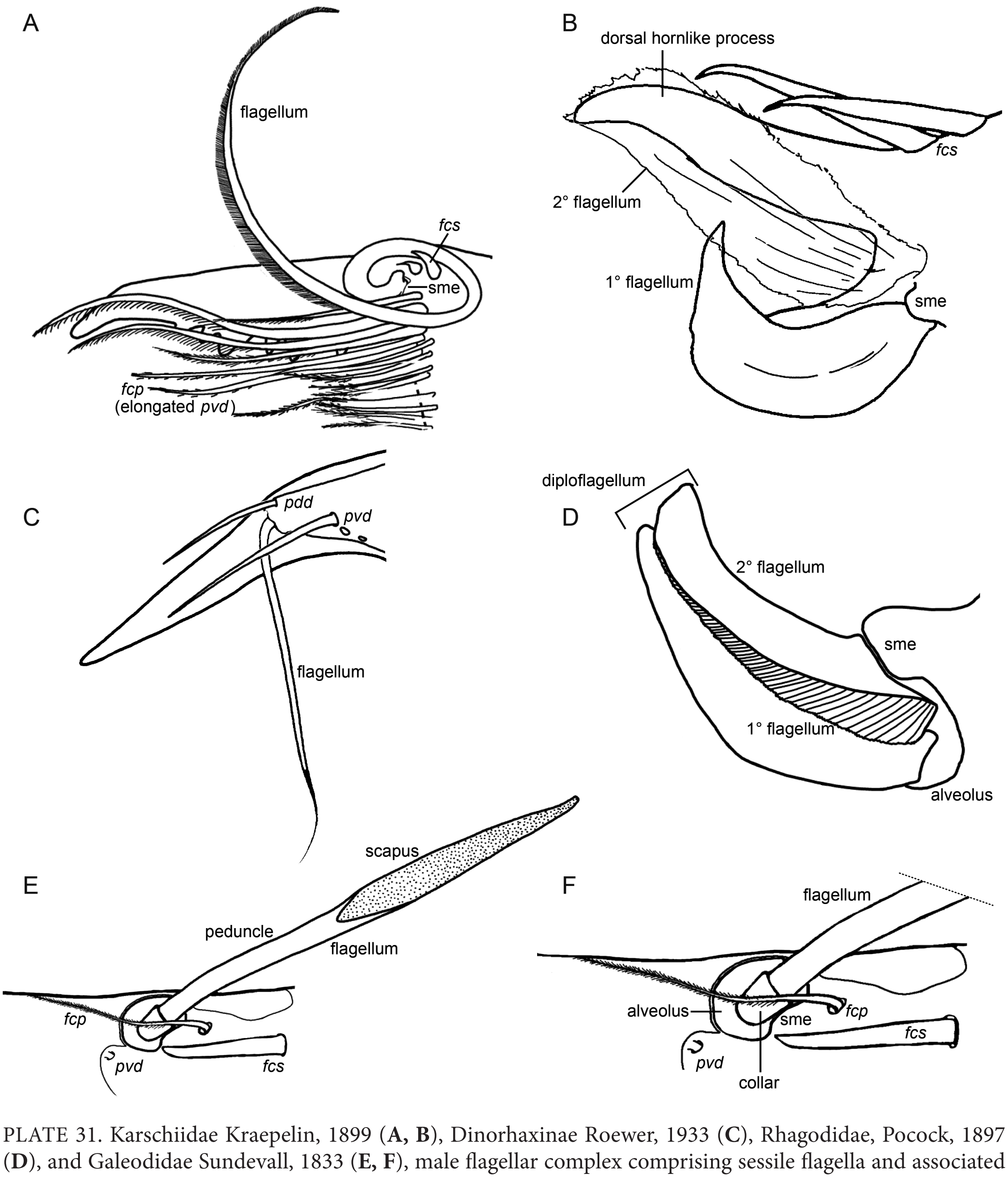

A
flagellum
fcs
sme
fcp
(elongated pvd)
B
dorsal hornlike process
fcs
2° flagellum
1° flagellum
sme
C
pdd
pvd
flagellum
D
diploflagellum
2° flagellum
sme
1° flagellum
alveolus
E
scapus
peduncle
flagellum
fcp
pvd
fcs
F
flagellum
alveolus
fcp
sme
fcs
pvd
collar

PLATE 31. Karschiidae Kraepelin, 1899 (**A, B**), Dinorhaxinae Roewer, 1933 (**C**), Rhagodidae, Pocock, 1897 (**D**), and Galeodidae Sundevall, 1833 (**E, F**), male flagellar complex comprising sessile flagella and associated setae, prolateral views. **A.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]). **B.** *Eusimonia nigrescens* Kraepelin, 1899, ♂ (AMNH [LP 7473]). **C.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **D.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW 14226). **E, F.** *Galeodes olivieri* Simon 1879, ♂ (AMNH [LP 4630]). Abbreviations: ***fcp*,** flagellar complex plumose setae; ***fcs*,** flagellar complex subspiniform to spiniform setae; ***pdd*,** prodorsal distal setae; ***pvd*,** proventral distal setae; **sme,** socket margin elevation; **1°,** primary; **2°,** secondary.

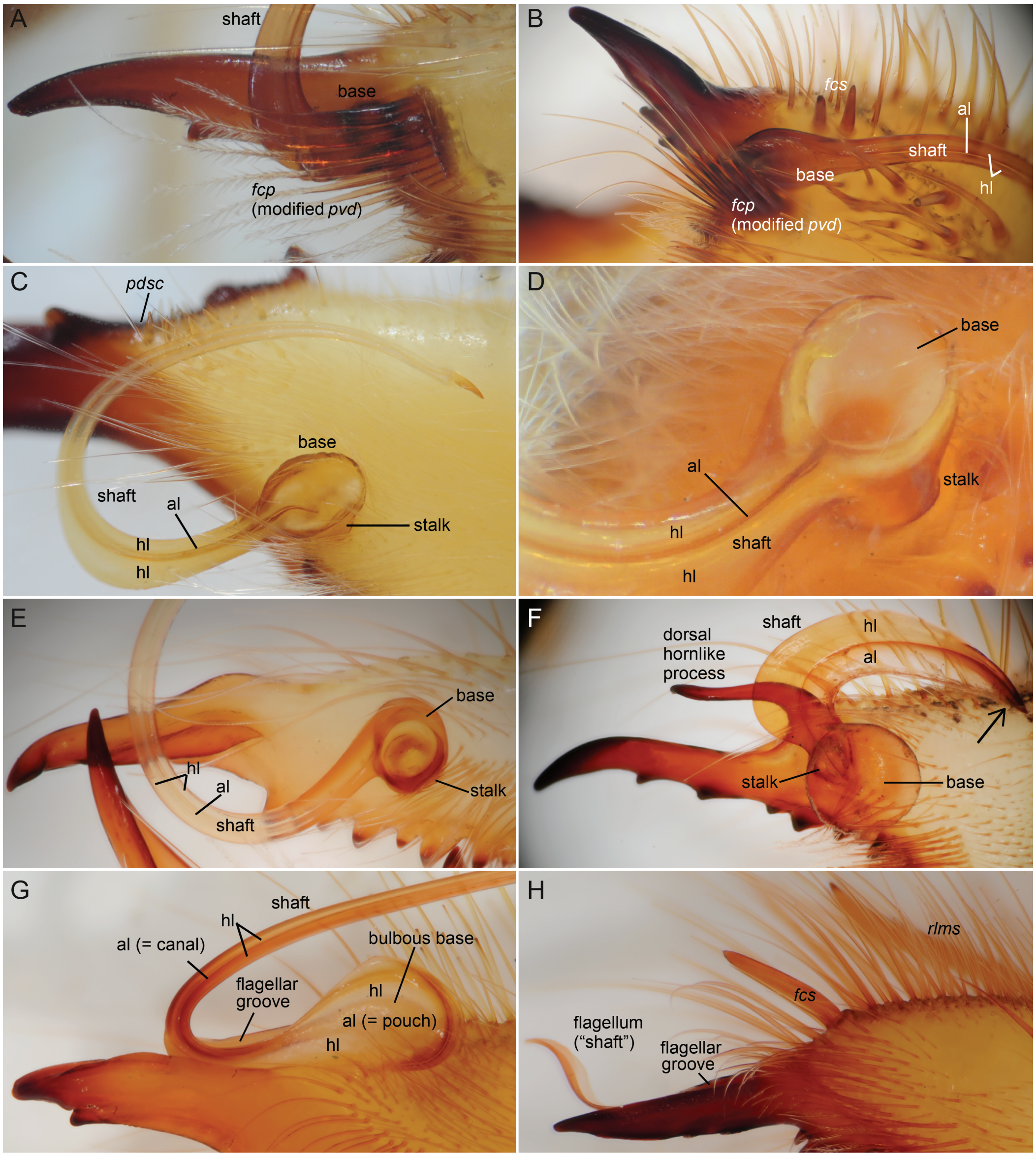

A
shaft
base
fcp
(modified pvd)
B
fcs
al
shaft
base
hl
fcp
(modified pvd)
C
pdsc
base
shaft
al
stalk
hl
hl
D
base
al
stalk
hl
shaft
hl
E
base
hl
al
stalk
shaft
F
dorsal
hornlike
process
shaft
hl
al
stalk
base
G
shaft
hl
al (= canal)
bulbous base
flagellar
groove
hl
al (= pouch)
hl
H
rlms
fcs
flagellum
("shaft")
flagellar
groove

PLATE 32. Ceromidae Roewer, 1933 (**A, B**), Hexisopodidae Pocock, 1897 (**C, D**), Daesiidae Kraepelin, 1899 (**E, F**), including Namibesiinae Wharton, 1981 (**E**), Solpugidae Leach, 1815 (**G**), and Gylippinae Roewer, 1933 (**H**), male flagellar complex comprising composite flagella and associated setae, prolateral (**A, C–H**) and prodorsal (**B**) views. **A.** *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355). **B.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **C.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). **D.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **E.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]). **F.** *Ammotrechelis goetschi* Roewer, 1934, ♂ (AMNH [LP 10673]). Arrow indicates external opening of putative alembic lumen (= alembic canal). **G.** *Solpuga chelicornis* Lichtenstein, 1796, ♂ (AMNH [LP 8158]). **H.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). Abbreviations: **al,** alembic lumen; ***fcp*,** flagellar complex plumose setae; ***fcs*,** flagellar complex subspiniform to spiniform setae; **hl,** hemolymph lumen; ***pdsc*,** prodorsal spiniform setal cluster; ***pvd*,** proventral distal setae; ***rlms*,** retrolateral manus spiniform seta.

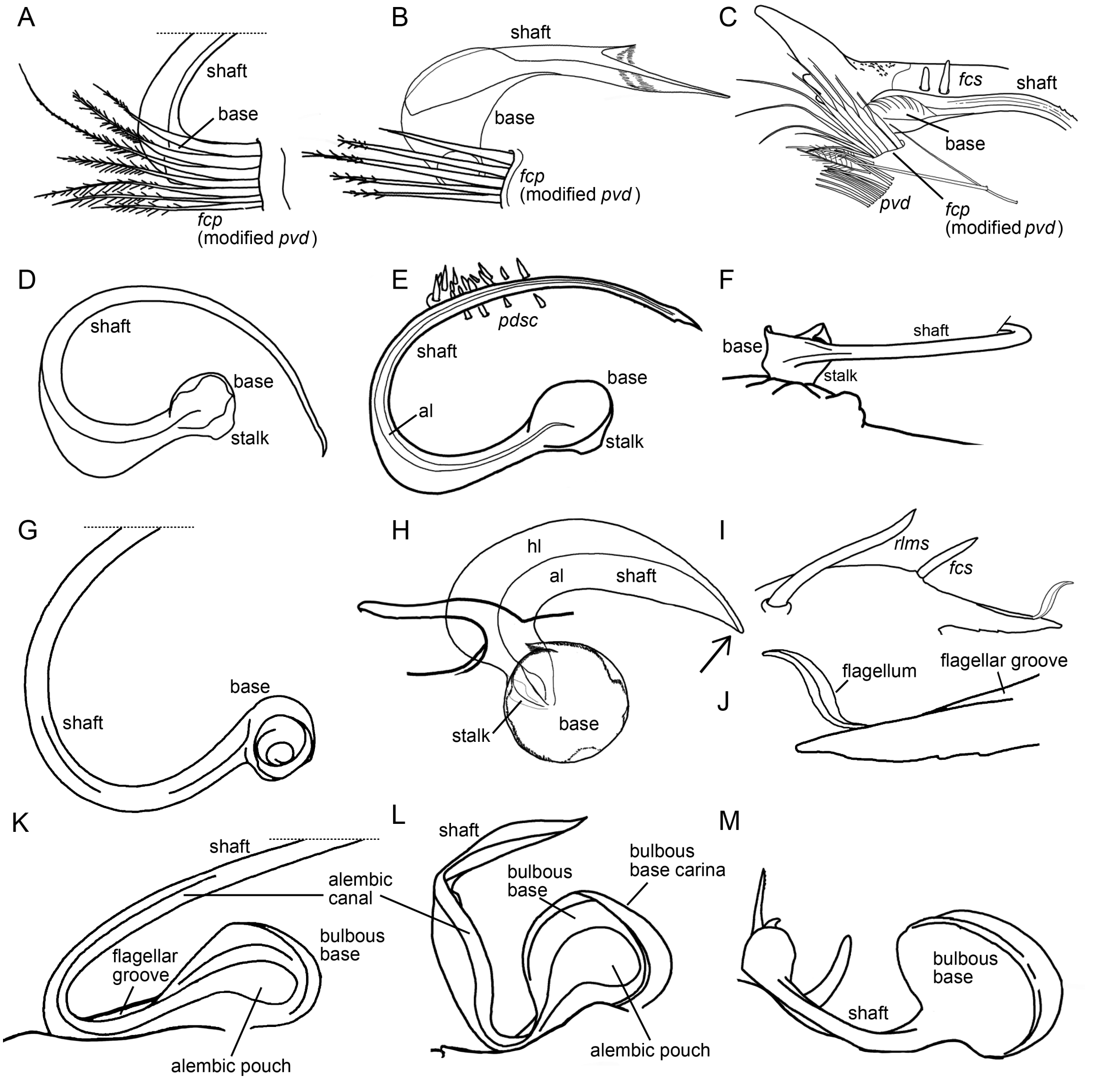

A
shaft
base
fcp
(modified pvd)
B
shaft
base
fcp
(modified pvd)
C
fcs
shaft
base
pvd
fcp
(modified pvd)
D
shaft
base
stalk
E
pdsc
shaft
al
base
stalk
F
base
shaft
stalk
G
base
shaft
H
hl
al
shaft
stalk
base
I
rlms
fcs
J
flagellum
flagellar groove
K
shaft
alembic canal
flagellar groove
bulbous base
alembic pouch
L
shaft
bulbous base
bulbous base carina
alembic pouch
M
bulbous base
shaft

PLATE 33. Ceromidae Roewer, 1933 (**A–C**), Hexisopodidae Pocock, 1897 (**D–F**), Daesiidae Kraepelin, 1899 (**G, H**), including Namibesiinae Wharton, 1981 (**G**), Gylippinae Roewer, 1933 (**I, J**), and Solpugidae Leach, 1815 (**K–M**), male flagellar complex comprising composite flagella and associated setae, prolateral (**A, B, D, E, G, H, J–M**), prodorsal (**C**), ventral (**F**), and retrolateral (**I**) views. **A.** *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355). **B.** *Ceromella* sp., ♂ (AMNH [LP 8527]). **C.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **D.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **E.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). **F.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426). **G.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]). **H.** *Ammotrechelis goetschi* Roewer, 1934, ♂ (AMNH [LP 10673]). Arrow indicates exterior opening of putative alembic lumen (= alembic canal). **I, J.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **K.** *Solpuga chelicornis* Lichtenstein, 1796, ♂ (AMNH [LP 8158]). **L.** *Solpugema genucornis* (Lawrence, 1935), ♂ (AMNH [LP 8167]). **M.** *Solpuguna* cf. *orangica*, ♂ (AMNH [LP 5969]). Abbreviations: **al,** alembic lumen; ***fcp*,** flagellar complex plumose setae; ***fcs*,** flagellar complex subspiniform to spiniform setae; **hl,** hemolymph lumen; ***pdsc*,** prodorsal spiniform setal cluster; ***pvd*,** proventral distal setae; ***rlms*,** retrolateral manus spiniform seta.

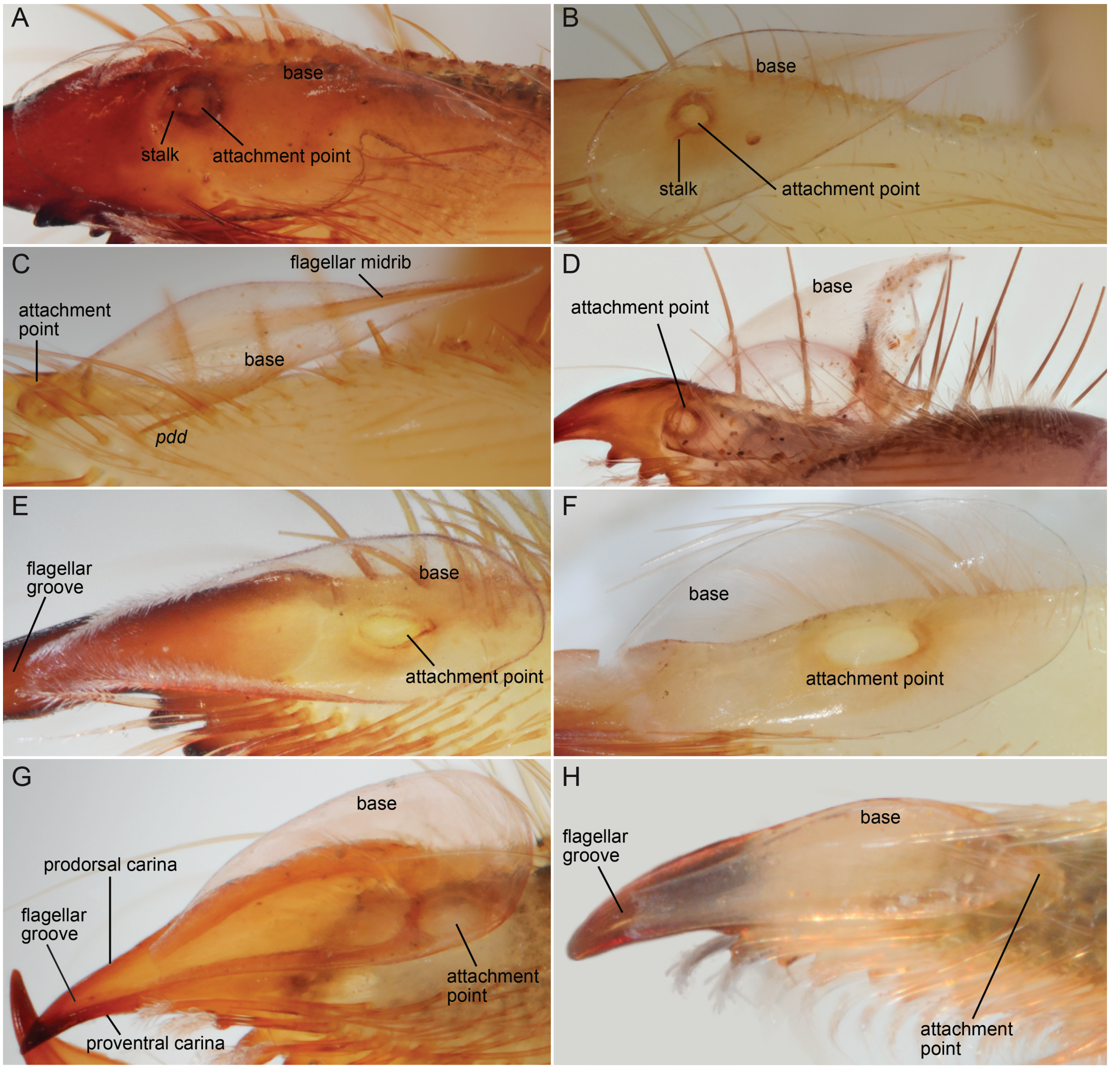

A
base
stalk
attachment point
B
base
stalk
attachment point
C
flagellar midrib
attachment point
base
pdd
D
base
attachment point
E
flagellar groove
base
attachment point
F
base
attachment point
G
base
prodorsal carina
flagellar groove
attachment point
proventral carina
H
base
flagellar groove
attachment point

PLATE 34. Daesiidae Kraepelin, 1899 (**A–D**), Ammotrechidae Roewer, 1934 (**E, F**), and Mummuciidae Roewer, 1934 (**G, H**), composite flagella, prolateral views, indicating membranous husk (**A–D**), bowl (**E, F**), and vesicle (**G, H**) shapes. **A.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **B.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♂ (AMNH [LP 3959]). **C.** *Blossia grandicornis* Lawrence, 1929, ♂ (AMNH [LP 5905]). **D.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **E.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **F.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]). **G.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]). **H.** *Uspallata* cf. *pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). Abbreviations: ***pdd*****,** prodorsal distal setae.

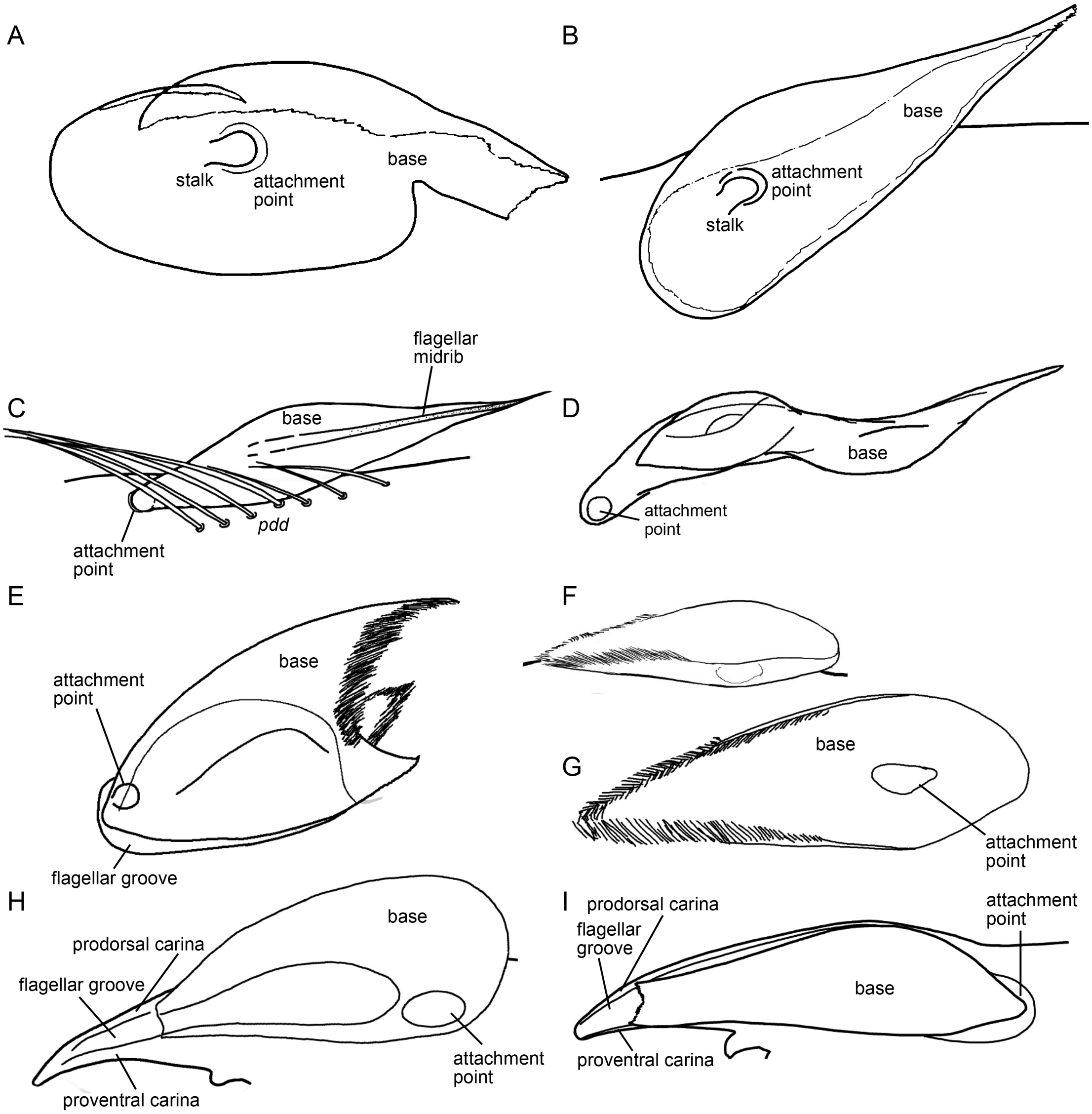

A
stalk
attachment point
base
B
base
attachment point
stalk
C
flagellar midrib
base
attachment point
pdd
D
base
attachment point
E
attachment point
base
flagellar groove
F
G
base
attachment point
H
base
prodorsal carina
flagellar groove
attachment point
proventral carina
I
prodorsal carina
flagellar groove
attachment point
base
proventral carina

PLATE 35. Daesiidae Kraepelin, 1899 (**A–E**), Ammotrechidae Roewer, 1934 (**F, G**), and Mummuciidae Roewer, 1934 (**H, I**), composite flagella, prolateral (**A–E, G–I**) and proventral (**F**) views, indicating membranous husk (**A–E**), bowl (**F, G**), and vesicle (**H, I**) shapes. **A.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **B.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♂ (AMNH [LP 3959]). **C.** *Blossia grandicornis* Lawrence, 1929, ♂ (AMNH [LP 5905]). **D.** *Hemiblossia australis* (Purcell, 1902), ♂ (AMNH [LP 9866]). **E.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **F, G.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **H.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]). **I.** *Uspallata* cf. *pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). Abbreviations: ***pdd*,** prodorsal distal setae.

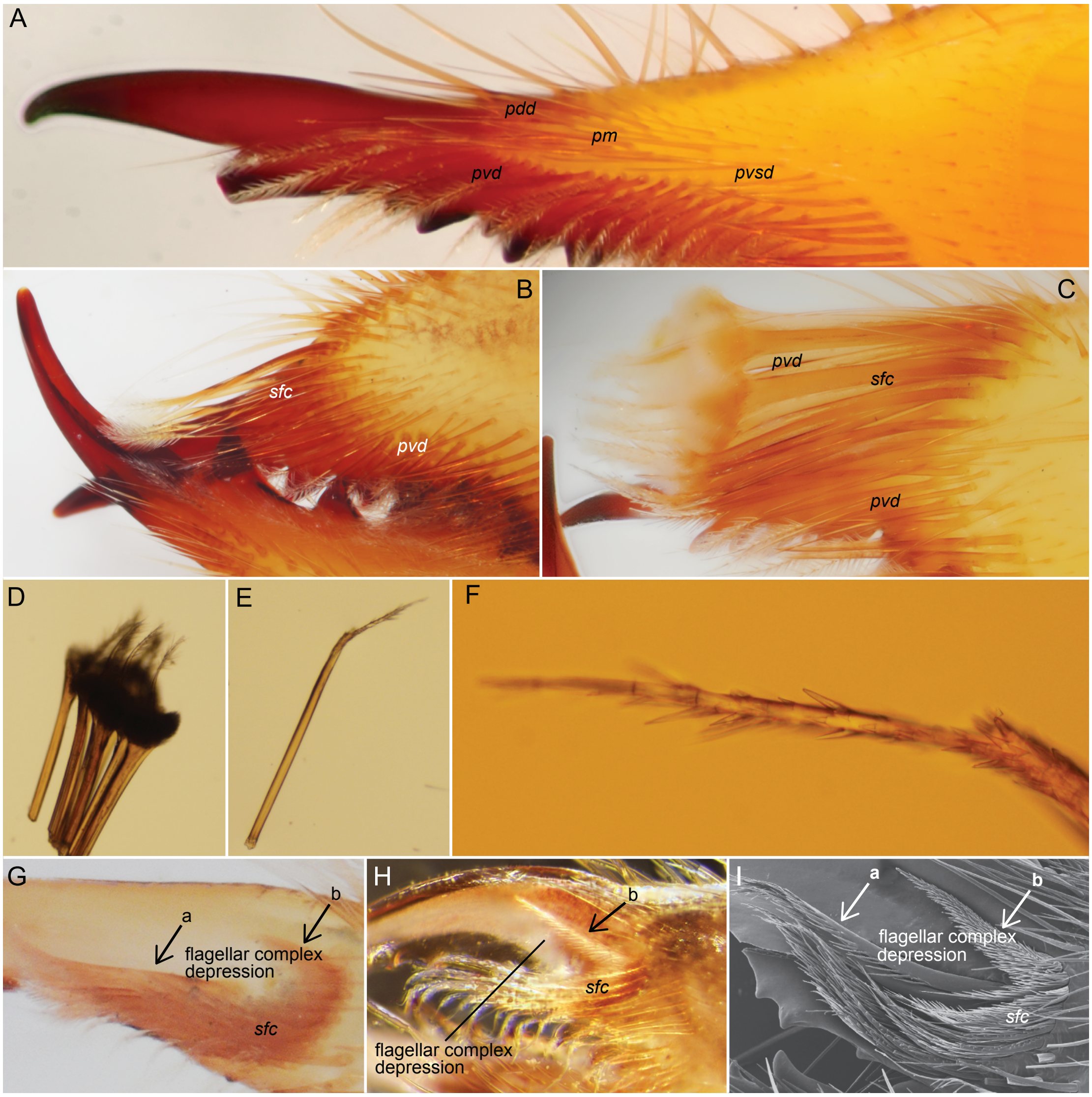

A
pdd
pm
pvd
pvsd
B
sfc
pvd
C
pvd
sfc
pvd
D
E
F
G
b
a
flagellar complex
depression
sfc
H
b
sfc
flagellar complex
depression
I
a
b
flagellar complex
depression
sfc

PLATE 36. Lipophaginae Wharton, 1981 (**A–F**) and Melanoblossiinae Roewer, 1933 (**G–I**), fixed fingers, prolateral views, indicating absent (**A**) and highly modified (**B, C**) *type B sfc* without a flagellum, comprising modified *pvd* setae (**D–F**), and *type C sfc* comprising modified *pvd* setae, prolateral views (**G–I**) indicating two distinctly differentiated setae (**a, b**), with seta "a" interpreted as homologous to primary flagellum of other solifuge families and seta "b" interpreted as *sfc principal seta*. **A.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (NMNW 12757). **B.** *Lipophaga trispinosa* Purcell, 1903, ♂ (NMNW 12503). **C–F.** *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601), with modified dorsal *pvd* setae fused apically (**D**), ventral, angular modified *pvd* setae, whole mount (**E**) and close-up (**F**). **G.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). **H.** *Melanoblossia braunsi* Purcell, 1903, ♂ (AMNH [LP 10737]). **I.** *Melanoblossia* sp., ♂ (NMNW 13396). Abbreviations: ***pdd*****,** prodorsal distal setae; ***pm*****,** promedial setae; ***pvd*****,** proventral distal setae; ***pvsd*****,** proventral subdistal setae; ***sfc*****,** setiform flagellar complex.

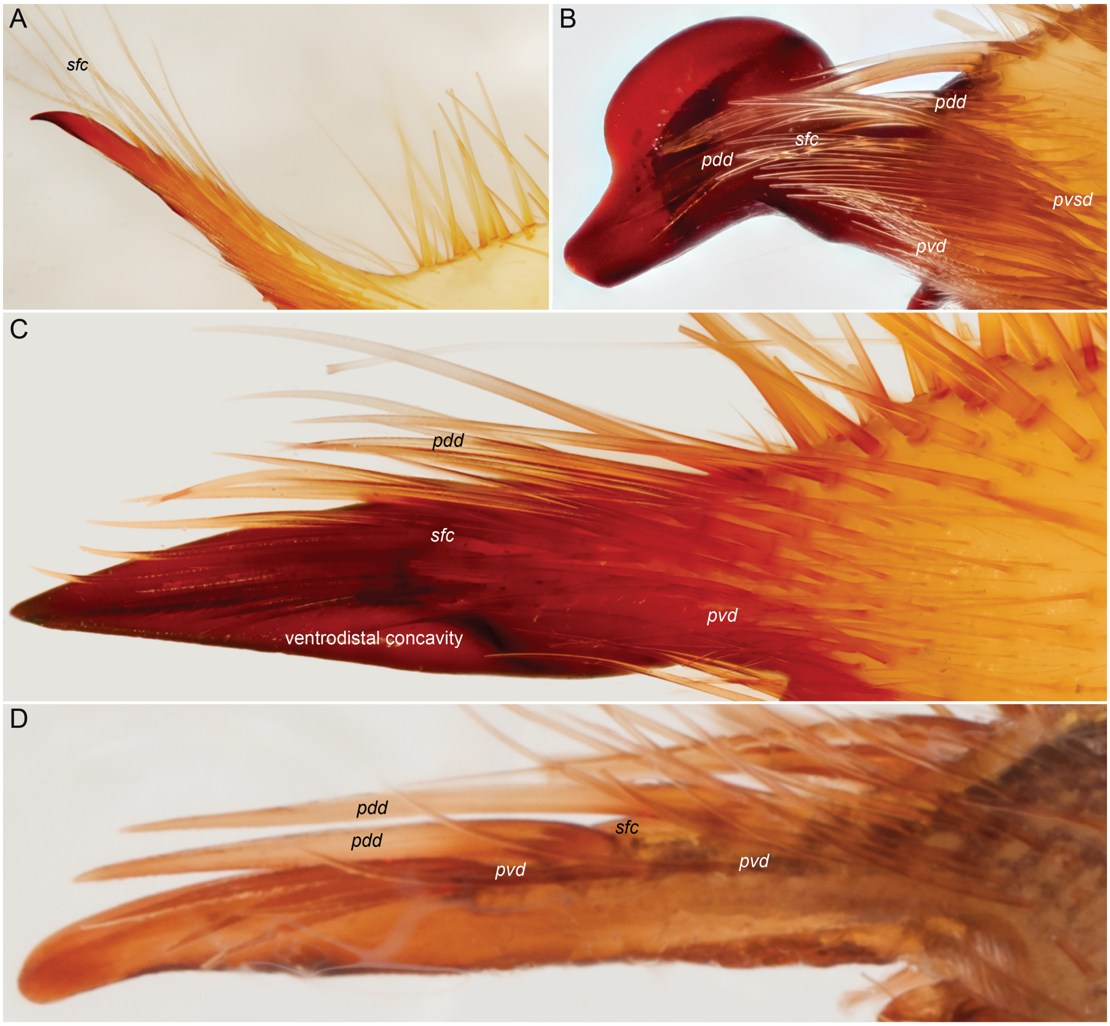

A
sfc
B
pdd
sfc
pdd
pvsd
pvd
C
pdd
sfc
pvd
ventrodistal concavity
D
pdd
pdd
sfc
pvd
pvd

PLATE 37. Eremobatidae Kraepelin, 1899, fixed fingers, prolateral views, indicating *type A sfc* comprising modified *pdd* and *pvd* setae, without a flagellum. **A.** *Chanbria regalis* Muma, 1951, ♂ (AMNH [LP10746]). **B.** *Eremothera sculpturata* Muma, 1951, ♂ (DMNS ZA.16475). **C.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]). Ventrodistal concavity opens retrolaterally; visible in prolateral view through semi-transparent fixed (dorsal) finger. **D.** *Hemerotrecha hanfordana* Brookhart and Cushing, 2008, holotype ♂ (DMNS ZA.21371). Abbreviations: ***pdd*,** prodorsal distal setae; ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae; ***sfc*,** setiform flagellar complex.

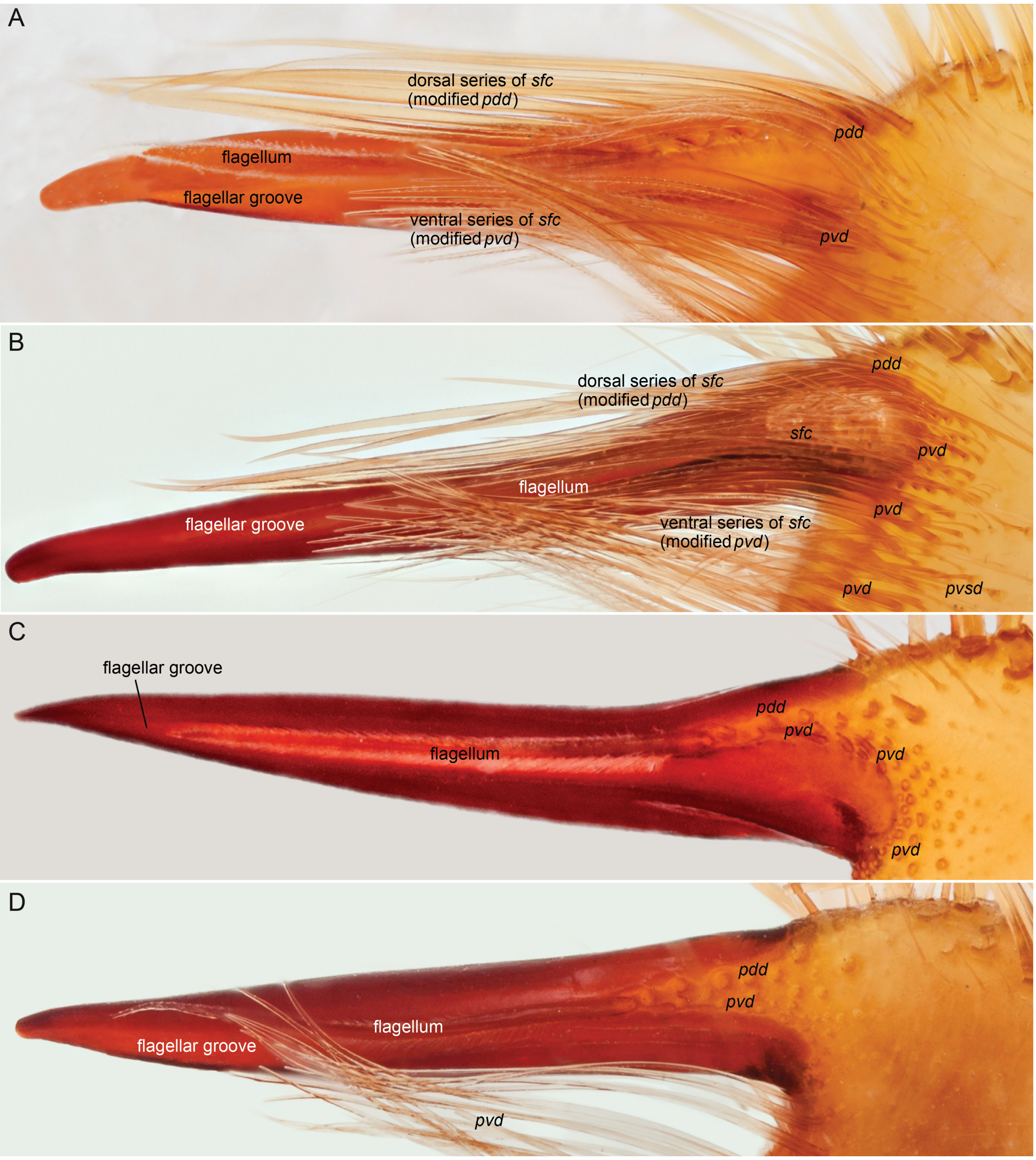

A
dorsal series of *sfc* (modified *pdd*)
pdd
flagellum
flagellar groove
ventral series of *sfc* (modified *pvd*)
pvd
B
pdd
dorsal series of *sfc* (modified *pdd*)
sfc
pvd
flagellum
flagellar groove
pvd
ventral series of *sfc* (modified *pvd*)
pvd
pvsd
C
flagellar groove
pdd
pvd
pvd
flagellum
pvd
D
pdd
pvd
flagellum
flagellar groove
pvd

PLATE 38. Eremobatidae Kraepelin, 1899, fixed fingers, prolateral views, indicating *type A sfc* comprising modified *pdd* and *pvd* setae, with a flagellum. **A.** *Eremobates ajoanus* Muma and Brookhart, 1988, paratype ♂ (DMNS ZA.17384). **B.** *Eremobates pallipes* (Say, 1823), ♂ (DMNS ZA.16258). **C.** *Eremobates gerbae* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10000). **D**. *Eremobates angustus* Muma, 1951, paratype ♂ (DMNS ZA.16789). Abbreviations: ***pdd*****,** prodorsal distal setae; ***pvd*****,** proventral distal setae; ***pvsd*****,** proventral subdistal setae; ***sfc*****,** setiform flagellar complex.

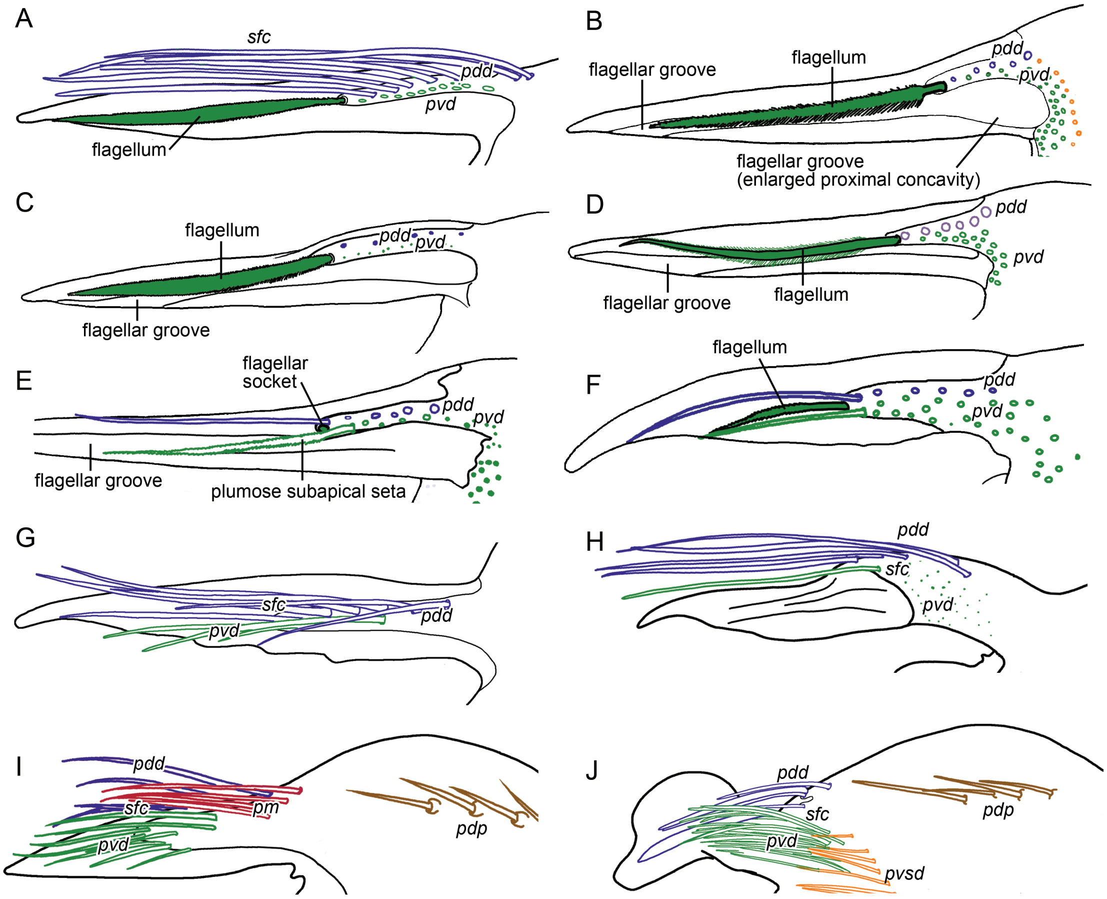
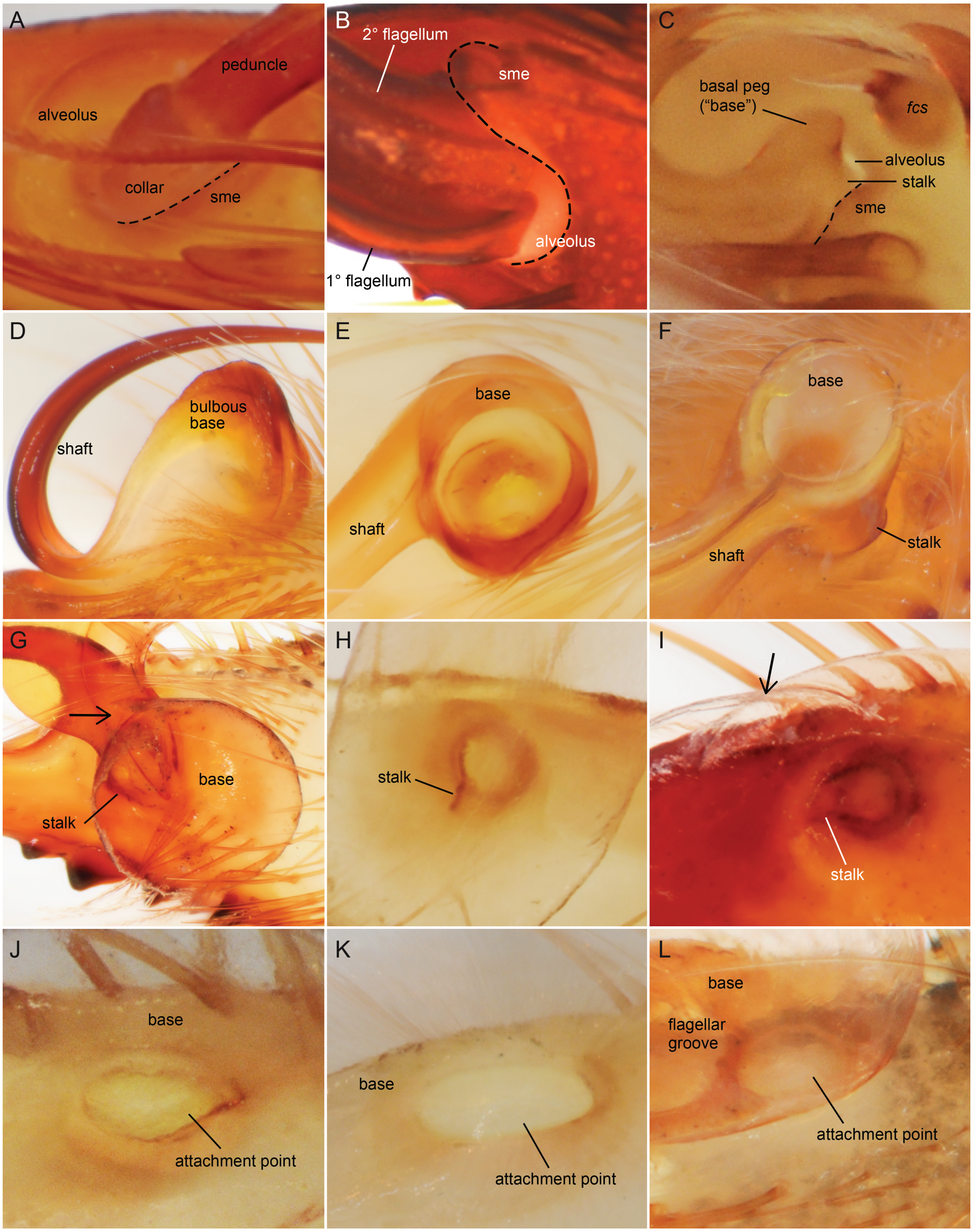

A
sfc
pdd
pvd
flagellum
B
flagellar groove
flagellum
pdd
pvd
flagellar groove
(enlarged proximal concavity)
C
flagellum
pdd
pvd
flagellar groove
D
pdd
pvd
flagellar groove
flagellum
E
flagellar
socket
pdd
pvd
flagellar groove
plumose subapical seta
F
flagellum
pdd
pvd
G
sfc
pvd
pdd
H
pdd
sfc
pvd
I
pdd
sfc
pm
pvd
pdp
J
pdd
sfc
pvd
pvsd
pdp

PLATE 39. Eremobatidae Kraepelin, 1899, fixed fingers, prolateral views, indicating *type A sfc* comprising modified *pdd* and *pvd* setae, with (**A–F**) or without (**G–J**) a flagellum (modified apical seta). **A.** *Eremobates bajadae* Muma and Brookhart, 1988, ♂ (AMNH [LP 5740]). **B.** *Eremobates gerbae* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10000). **C.** *Eremobates* cf. *palpisetulosus*, ♂ (AMNH), Mexico: Coahuila. **D.** *Eremobates angustus* Muma, 1951, paratype ♂ (DMNS ZA.16789). **E.** *Eremobates chihuaensis* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10002). **F.** *Eremochelis oregonensis* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10008). **G.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH). **H.** *Eremochelis bilobatus* (Muma, 1951), ♂ (DMNS ZA.16039). **I.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]). **J.** *Eremothera sculpturata* Muma, 1951, ♂ (DMNS ZA.16475). Flagellum colored solid green. Abbreviations: ***pdd*,** prodorsal distal setae (blue); ***pdp*,** prodorsal proximal setae (brown); ***pm*,** promedial setae (red); ***pvd*,** proventral distal setae (green); ***pvsd*,** proventral subdistal setae (orange); ***sfc*,** setiform flagellar complex.


A
peduncle
alveolus
collar
sme
B
2° flagellum
sme
alveolus
1° flagellum
C
basal peg
("base")
fcs
alveolus
stalk
sme
D
bulbous
base
shaft
E
base
shaft
F
base
stalk
shaft
G
base
stalk
H
stalk
I
stalk
J
base
attachment point
K
base
attachment point
L
base
flagellar
groove
attachment point

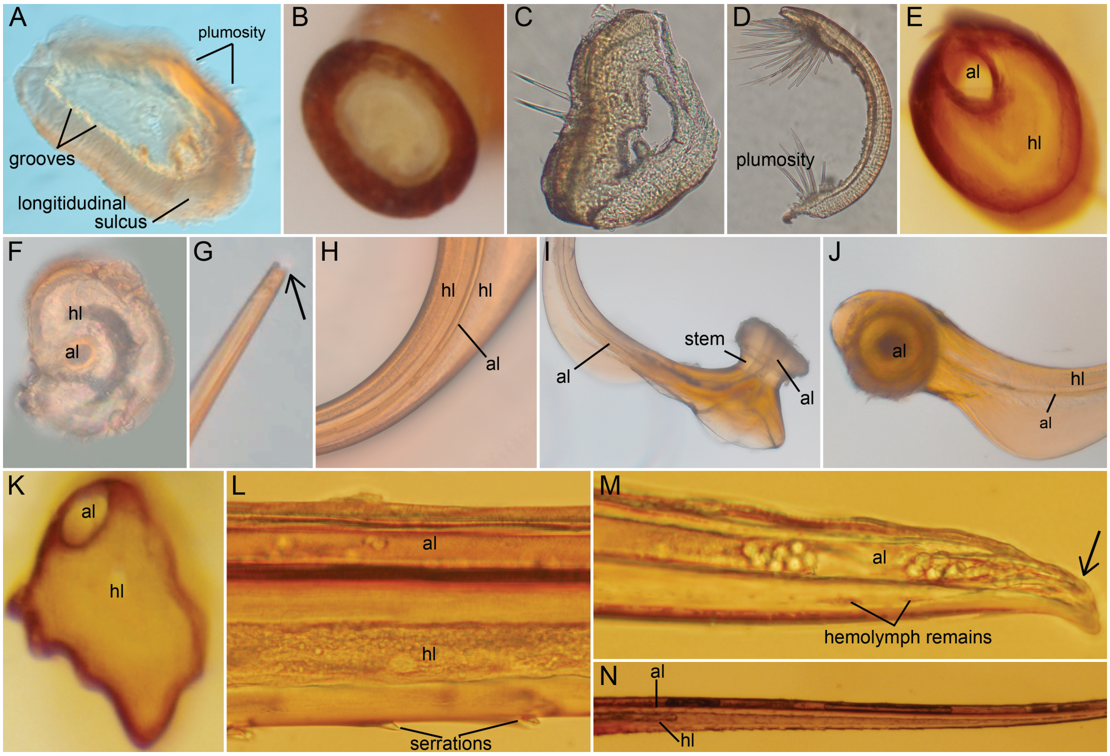


PLATE 41. Dinorhaxinae Roewer, 1933 (**A**), Galeodidae Sundevall, 1833 (**B–D**), Solpugidae Leach, 1815 (**E**), Hexisopodidae Pocock, 1897 (**F–J**), and Ceromidae Roewer, 1933 (**K–N**), male flagella, cross sections through filiform flagellum (**A**), peduncle (**B**), peduncle near transition to scapus (**C**), scapus (**D**), and shaft (**E, F, K**), and whole mount (**G–J, L–N**), indicating alembic lumen (= alembic canal) (**E–N**) apparently opening externally at apex (**G, M,** arrows) and broad hemolymph lumen near base (**E–N**), narrowing and eventually disappearing toward apex (**M**). **A.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (MRAC), Vietnam: Cauda Nhatray. **B–D.** *Galeodes turkestanus* Kraepelin, 1899, ♂ (AMNH), Uzbekistan: Dikhana Canyon. **E.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]). **F–J.** *Hexisopus* sp., ♂ (NMNW 13179). **K–N.** *Ceroma inerme* Purcell, 1899, ♂ (NMNW 13632). Abbreviations: **al,** alembic lumen; **hl,** hemolymph lumen.

←

PLATE 40. Galeodidae Sundevall, 1833 (**A**), Rhagodidae Pocock, 1897 (**B**), Karschiidae Kraepelin, 1899 (**C**), Solpugidae Leach, 1815 (**D**), Daesiidae Kraepelin, 1899 (**E, G–I**), including Namibesiinae Wharton, 1981 (**E**), Hexisopodidae Pocock, 1897 (**F**), Ammotrechidae Roewer, 1934 (**J, K**), and Mummuciidae Roewer, 1934 (**L**), flagellar attachment points, prolateral views, of flagella movably (**A, C, E–I**) and immovably (**B, D, J–L**) fixed to cheliceral finger. **A.** *Galeodes olivieri* Simon 1879, ♂ (AMNH [LP 4630]). **B.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW 14226). **C.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]). **D.** *Solpugyla* sp., ♂ (AMNH [LP 10764]). **E.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]). **F.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). **G.** *Ammotrechelis goetschi* Roewer, 1934, ♂ (AMNH [LP 10673]). **H.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♂ (AMNH [LP 3959]). **I.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **J.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **K.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]). **L.** *Uspallata* cf. *pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). Arrows (**G, I**) indicate overlapping margins of membranous base. Abbreviations: ***fcs,*** flagellar complex subspiniform seta; **sme,** socket margin elevation.; **1°,** primary; **2°,** secondary.

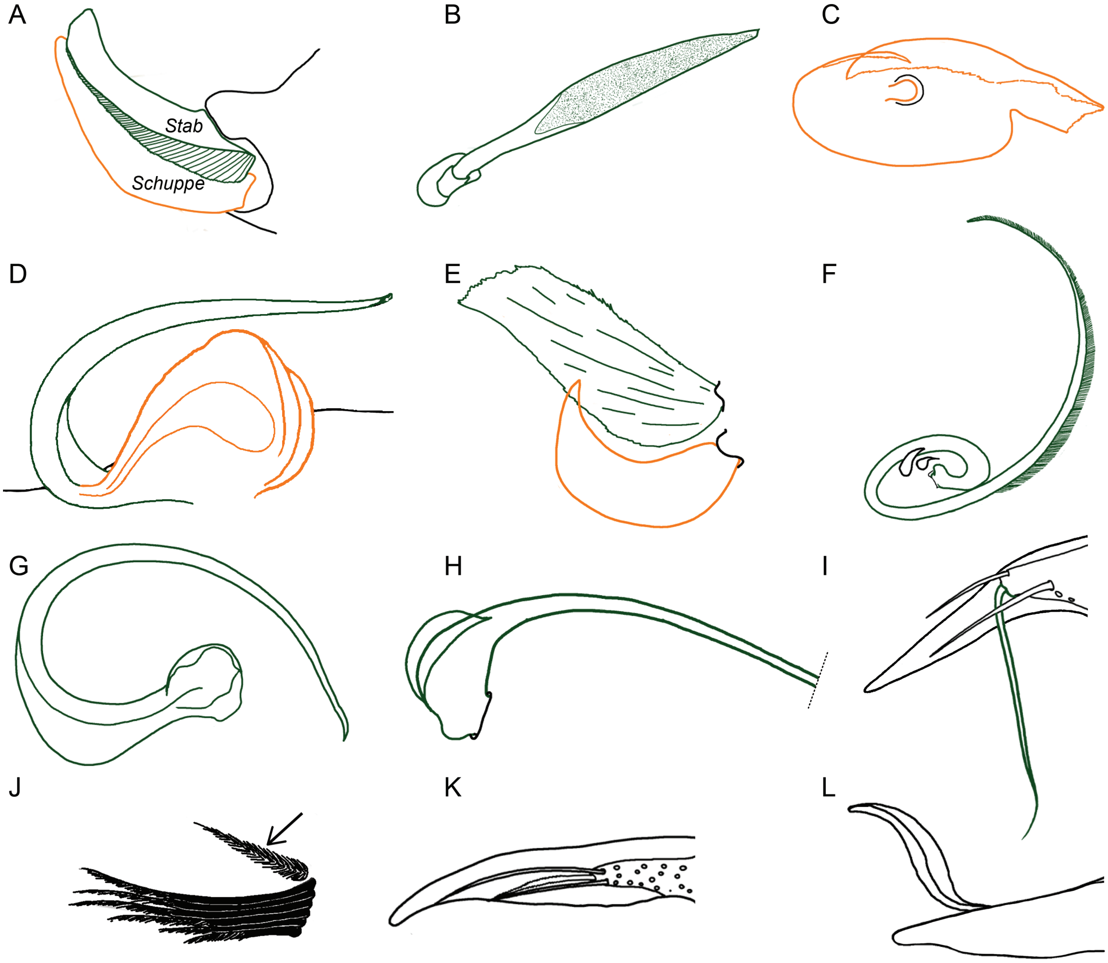


PLATE 42. Rhagodidae Pocock, 1897 (**A**), Galeodidae Sundevall, 1833 (**B**), Daesiidae Kraepelin, 1899 (**C**), Solpugidae Leach, 1815 (**D**), Karschiidae Kraepelin, 1899 (**E, F**), *Eusimonia* Kraepelin, 1899 (**E**) and *Karschia* Walter, 1889 (**F**), Hexisopodidae Pocock, 1897 (**G**), Ceromidae Roewer, 1933 (**H**), Dinorhaxinae Roewer, 1933 (**I**), Melanoblossiinae Roewer, 1933 (**J**), Eremobatidae Kraepelin, 1899 (**K**), and Gylippinae Roewer, 1933 (**L**), schematic representation of Kraepelin's (1908a) hypotheses of flagellar origin based on the two rhagodid flagella, termed the *Stab* ("rod"; colored green) and *Schuppe* ("flake"; colored orange). Arrow indicates seta historically interpreted as flagellum of Melanoblossiinae.

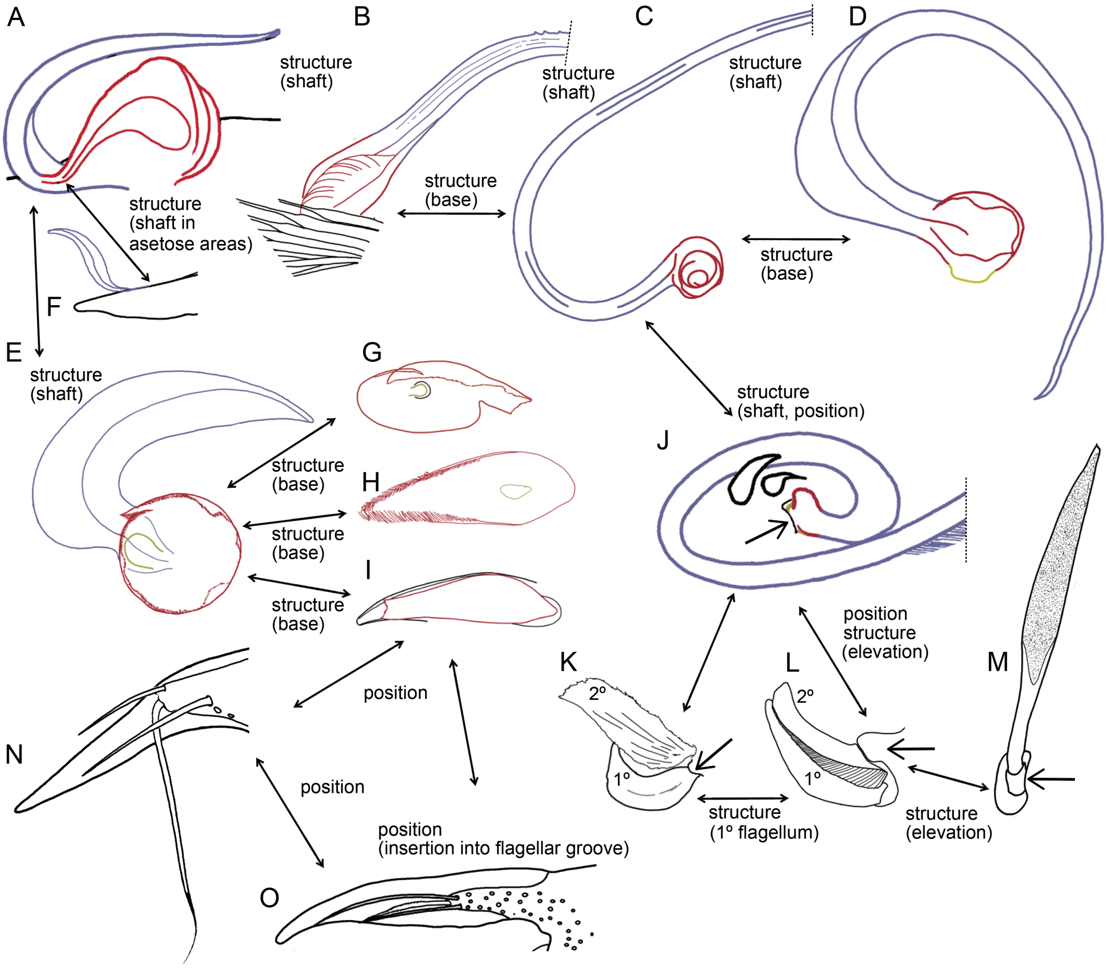

A
B
C
D
structure (shaft)
structure (shaft)
structure (shaft)
structure (base)
structure (shaft in asetose areas)
structure (base)
F
E
structure (shaft)
G
structure (shaft, position)
structure (base)
H
J
structure (base)
I
structure (base)
position structure (elevation)
position
K
L
M
2°
2°
N
1°
1°
position
structure (1° flagellum)
structure (elevation)
position (insertion into flagellar groove)
O

PLATE 43. Solpugidae Leach, 1815 (**A**), Ceromidae Roewer, 1933 (**B**), Daesiidae Kraepelin, 1899 (**C, E, G**), including Namibesiinae Wharton, 1981 (**C**) and *Ammotrechelis goetschi* Roewer, 1934 (**E**), Hexisopodidae Pocock, 1897 (**D**), Gylippinae Roewer, 1933 (**F**), Ammotrechidae Roewer, 1934 (**H**), Mummuciidae Roewer, 1934 (**I**), Karschiidae Kraepelin, 1899, *Karschia* Walter, 1889 (**J**) and *Eusimonia* Kraepelin, 1899 (**K**), Rhagodidae Pocock, 1897 (**L**), Galeodidae Sundevall, 1833 (**M**), Dinorhaxinae Roewer, 1933 (**N**), and Eremobatidae Kraepelin, 1899 (**O**), schematic representations of hypothesized single origin of primary flagellum based on structural and positional hypotheses of primary homology. Parts of composite flagella and sessile flagellum of *Karschia* hypothesized to be homologous are colored maroon (flagellar base) and violet (flagellar shaft). Short arrows indicate flagellar socket margin elevation (sme); long arrows indicate structural or positional similarity. Abbreviations: **1°**, primary; **2°**, secondary.

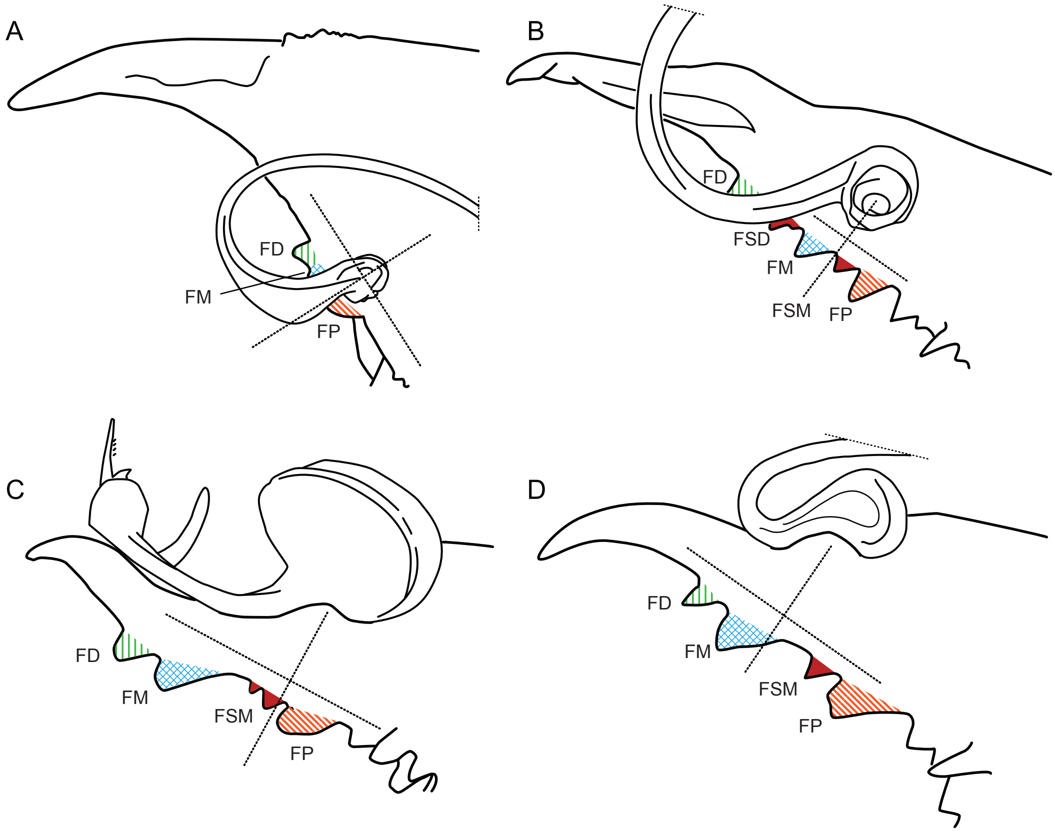


PLATE 44. Hexisopodidae Pocock, 1897 (**A**), Namibesiinae Wharton, 1981 (**B**), and Solpugidae Leach, 1815 (**C, D**), fixed fingers, prolateral views, indicating point of attachment of flagellum relative to teeth. **A.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426). **B.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]), **C.** *Solpuguna* cf. *orangica*, ♂ (AMNH [LP 5969]). **D.** *Zeria keyserlingi* (Pocock, 1895), ♂ (AMNH [LP 4632]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth/teeth.

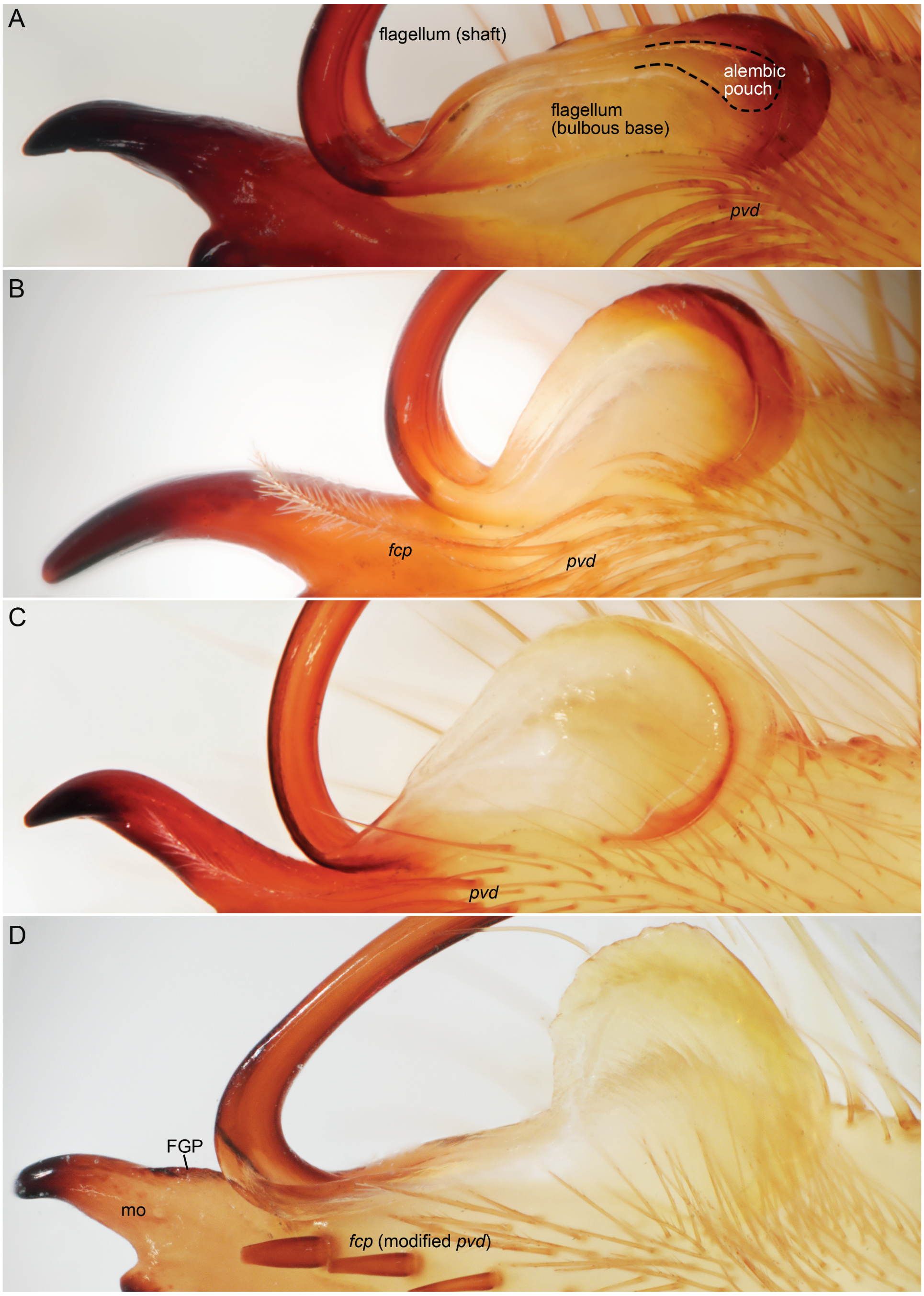

A
flagellum (shaft)
alembic pouch
flagellum (bulbous base)
pvd
B
fcp
pvd
C
pvd
D
FGP
mo
fcp (modified *pvd*)

PLATE 45. Solpugidae Leach, 1815, fixed finger, prolateral views, indicating proventral distal (*pvd*) setae at base of flagellum, and flagellar attachment point relative to *pvd* setae. **A.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **B.** *Zeria adunca* (Roewer, 1933), ♂ (MRAC 216.105). **C.** *Solpugassa furcifera* (Kraepelin, 1899), ♂ (AMNH [LP 3632]). **D.** *Oparba asiatica* (Turk, 1948), ♂ (HUJI 360). Abbreviations: **FGP,** flagellar groove process; ***fcp*,** flagellar complex plumose seta/e; **mo,** mucron organ; ***pvd*,** proventral distal setae.

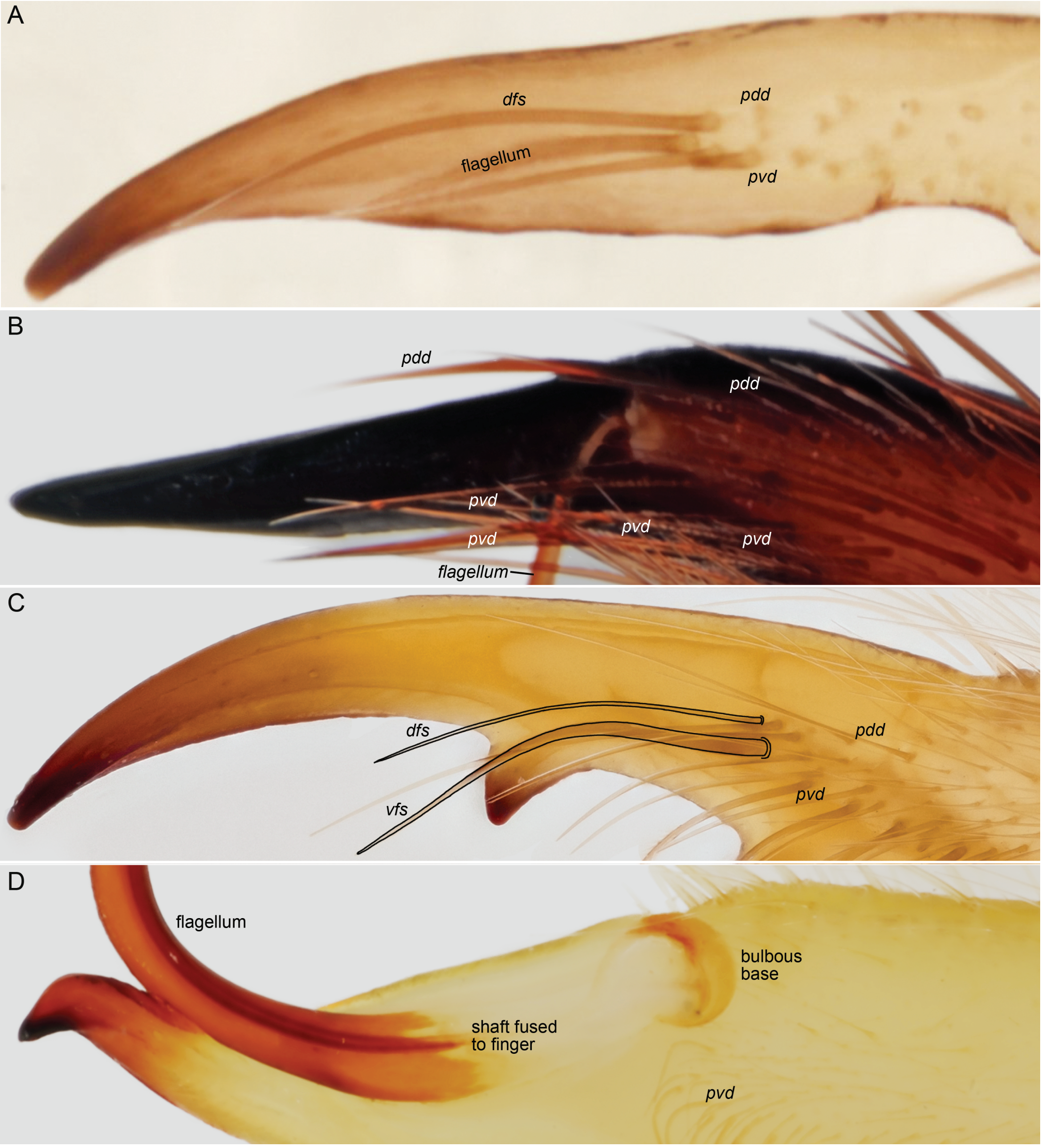

A
dfs
pdd
flagellum
pvd
B
pdd
pdd
pvd
pvd
pvd
pvd
flagellum
C
dfs
pdd
vfs
pvd
D
flagellum
bulbous base
shaft fused to finger
pvd

PLATE 46. Eremobatidae Kraepelin, 1899 (**A**), Dinorhaxinae Roewer, 1933 (**B**), and Solpugidae Leach, 1815 (**C, D**), cheliceral fixed finger, prolateral views, indicating distal setae. **A.** *Eremochelis oregonensis* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10008). **B.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **C, D.** *Metasolpuga picta* (Kraepelin, 1899), subad. ♂ (AMNH), Namibia: Gobabeb (**C**), and ♂ (AMNH [LP 10719]) (**D**). Abbreviations: ***dfs*,** dorsal flagellar seta; ***pdd*,** prodorsal distal setae; ***pvd*,** proventral distal setae; ***vfs*,** ventral flagellar seta.

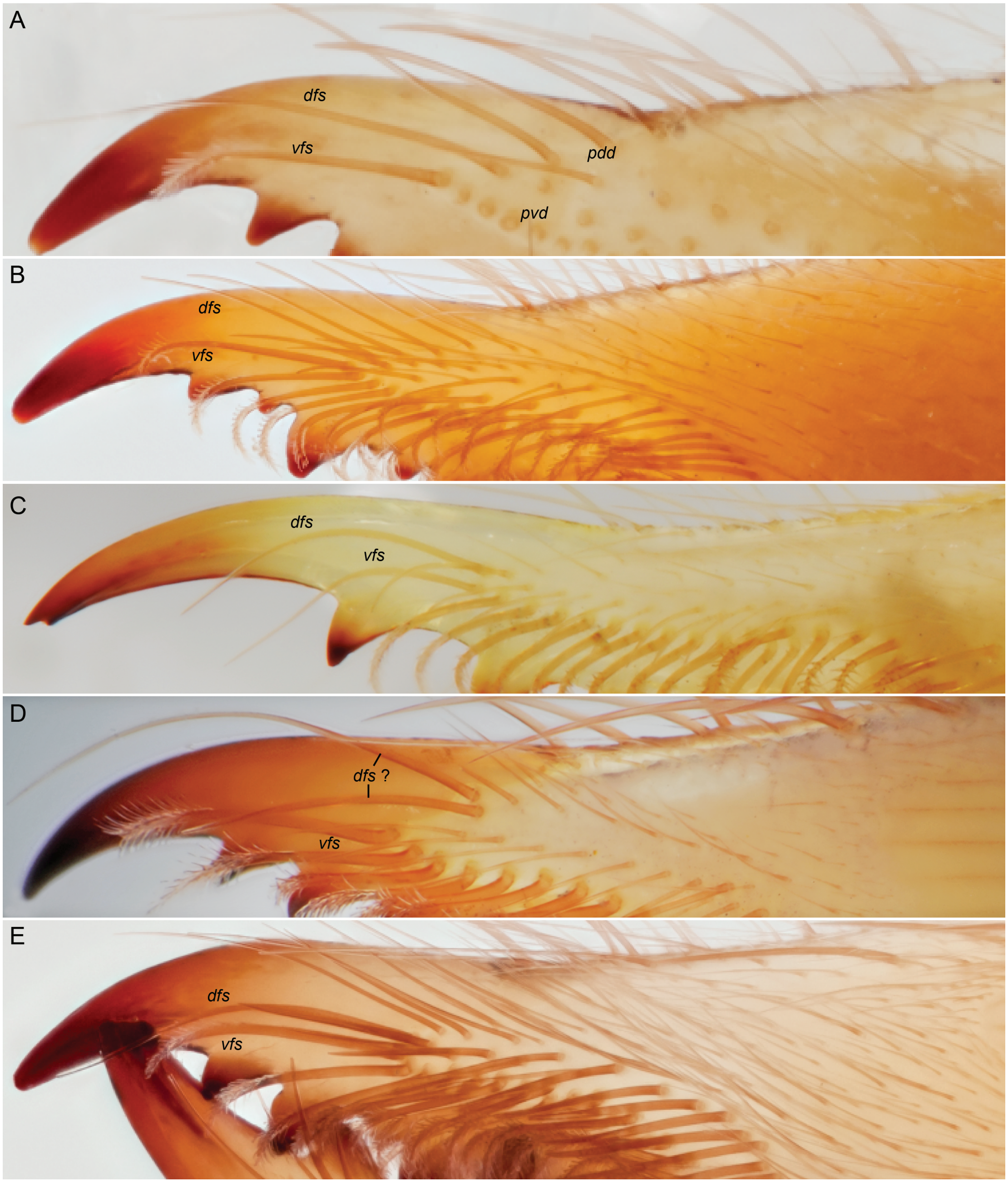


PLATE 47. Eremobatidae Kraepelin, 1899 (**A, B**), Solpugidae Leach, 1815 (**C**), and Daesiidae Kraepelin, 1899 (**E, F**), cheliceral fixed finger, prolateral views, indicating apicalmost setae. **A.** *Hemerotrecha sevilleta* Brookhart and Cushing, 2002, allotype ♀ (DMNS ZA.10007). **B.** *Eremochelis insignatus* Roewer, 1934, ♀ (DMNS ZA.16136). **C.** *Prosolpuga schultzei* (Kraepelin, 1908), ♀ (AMNH [LP 3605]). **D.** *Blossia grandicornis* Lawrence, 1929, ♀ (AMNH [LP 5905]), indicating two potential *dfs*. **E.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♀ (AMNH [LP 3959]). Abbreviations: ***dfs*,** dorsal flagellar seta; ***pdd*,** prodorsal distal setae; ***pvd*,** proventral distal setae; ***vfs*,** ventral flagellar seta.

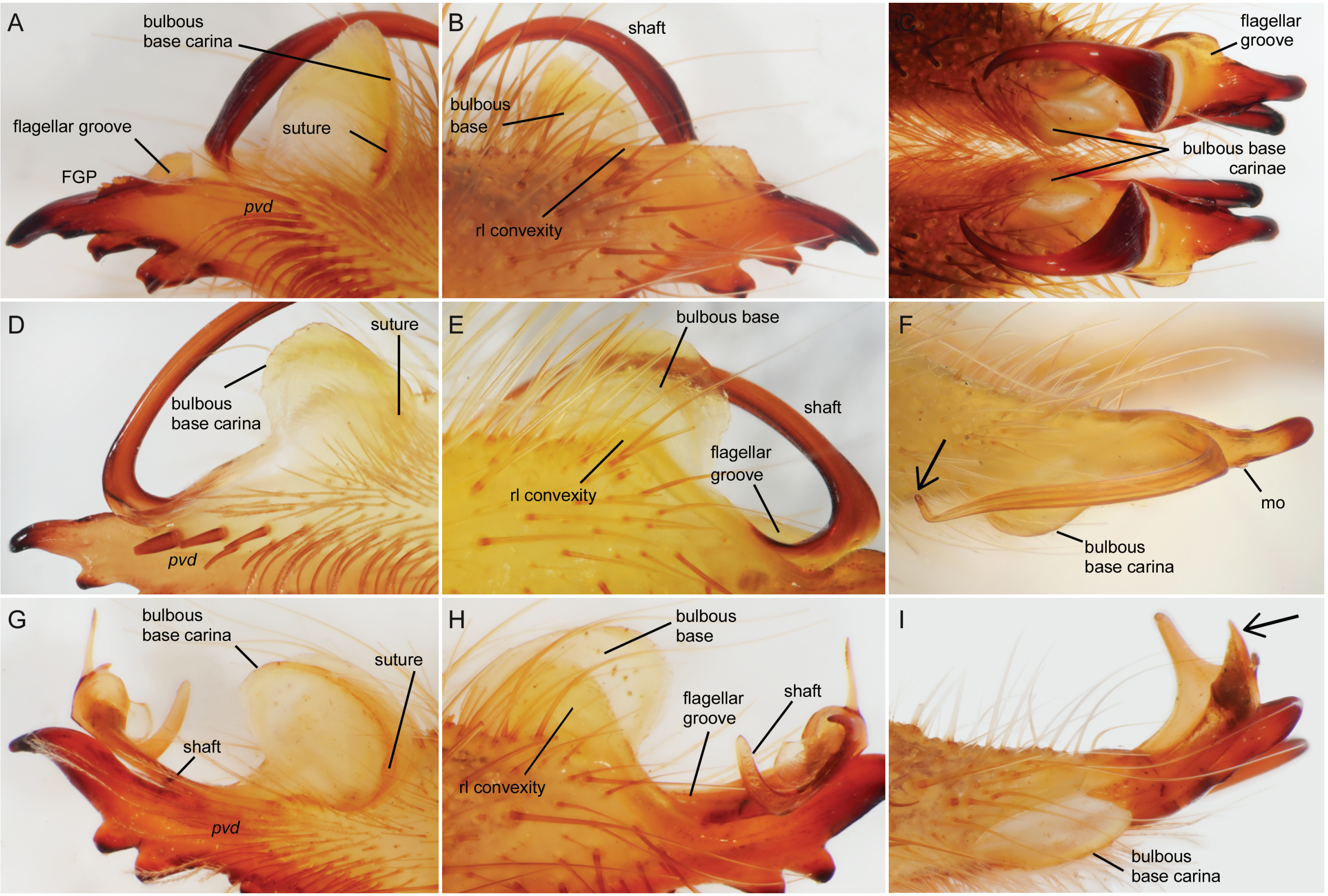

A
bulbous base carina
flagellar groove
suture
FGP
pvd
B
shaft
bulbous base
rl convexity
C
flagellar groove
bulbous base carinae
D
suture
bulbous base carina
pvd
E
bulbous base
shaft
flagellar groove
rl convexity
F
mo
bulbous base carina
G
bulbous base carina
suture
shaft
pvd
H
bulbous base
flagellar groove
shaft
rl convexity
I
bulbous base carina

PLATE 48. Solpugidae Leach, 1815, cheliceral fixed finger, male flagellum, prolateral (**A, D, G**), retrolateral (**B, E, H**) and dorsal (**C, F, I**) views, indicating different aspects of bulbous base. **A–C.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). **D–F.** *Oparba asiatica* (Turk, 1948). **D, F.** Holotype ♂ (HUJI). **E.** ♂ (HUJI 360). **G–I.** *Solpuguna* cf. *orangica*, ♂ (AMNH [LP 5969]). Arrows indicate external opening of alembic lumen (= alembic canal). Abbreviations: **FGP,** flagellar groove process; **mo,** mucron organ; ***pvd*,** proventral distal setae; **rl,** retrolateral.

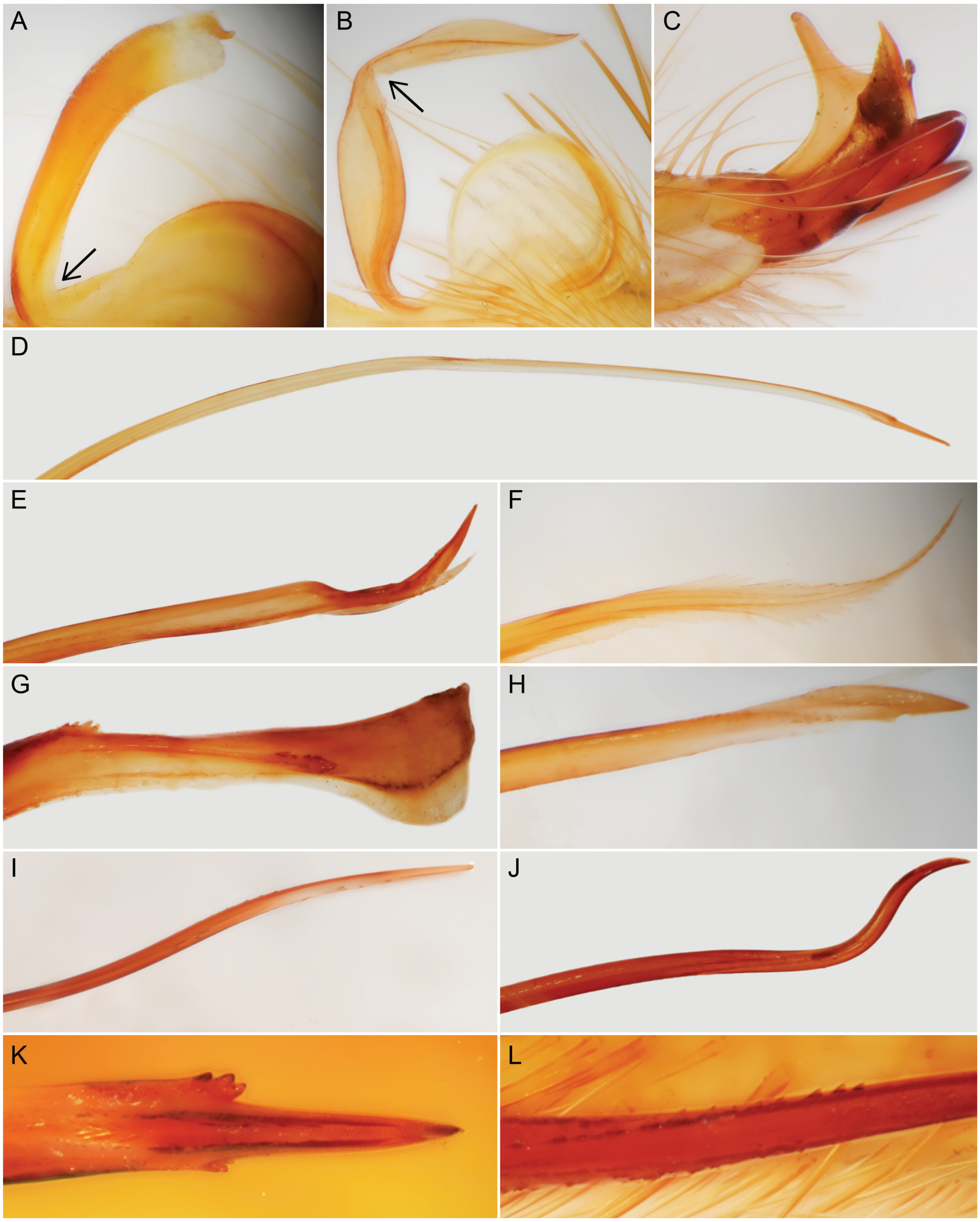


PLATE 49. Solpugidae Leach, 1815, male flagellum and flagellar shaft, prolateral (**A, B, D–J**) and dorsal (**C, K, L**) views, indicating diversity of shapes and microstructures. **A.** *Solpugella* sp., ♂ (NMNW 11097). **B.** *Solpugema genucornis* (Lawrence, 1935), ♂ (AMNH [LP 8167]). **C.** *Solpuguna* cf. *orangica*, ♂ (AMNH [LP 5969]). **D.** *Solpugista bicolor* (Lawrence, 1953), ♂ (AMNH [LP 7933]). **E.** *Solpugassa furcifera* (Kraepelin, 1899), ♂ (AMNH [LP 3632]). **F.** *Solpugiba lineata* (C.L. Koch, 1842), ♂ (AMNH [LP 5919]). **G.** *Zeria fordi* (Hirst, 1907), ♂ (AMNH [LP 9090]). **H.** *Zeria fusca* (C.L. Koch, 1842), ♂ (AMNH [LP 1473]). **I.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **J.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]). **K.** *Zeria lawrencei* (Roewer, 1933), ♂ (AMNH [LP 9906]). **L.** *Zeria keyserlingi* (Pocock, 1895), ♂ (AMNH [LP 4632]). Arrows indicate weakened area of cuticle on shaft (possible points of articulation).

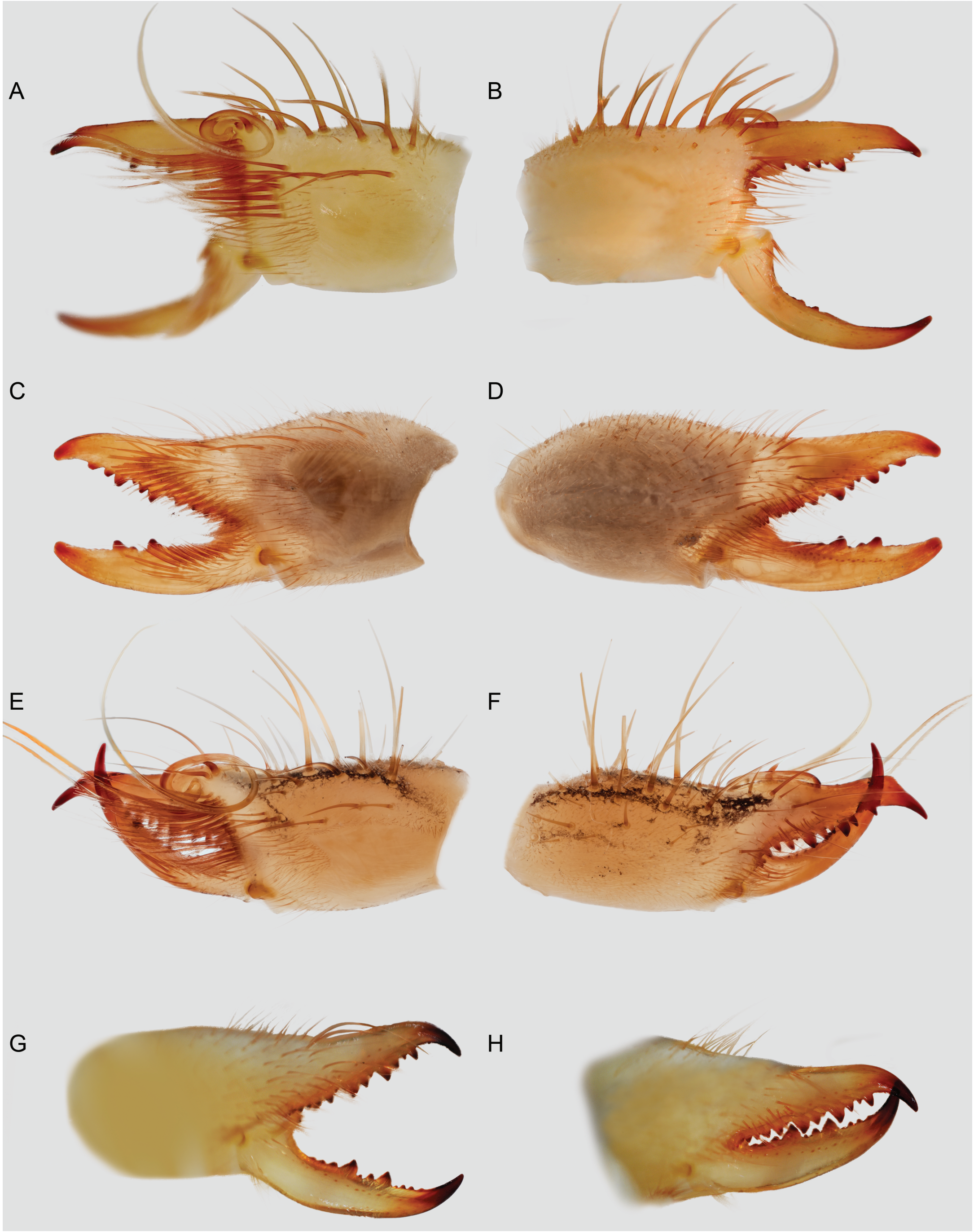


PLATE 50. Karschiidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D, F–H**) views. **A–D.** *Karschia* (*K.*) *mastigofera* Birula, 1890. **A, B.** ♂ (AMNH [LP 7474]). **C, D.** ♀ (AMNH [LP 7476]). **E, F.** *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **G, H.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]), with cheliceral fingers open (**G**) and closed (**H**).

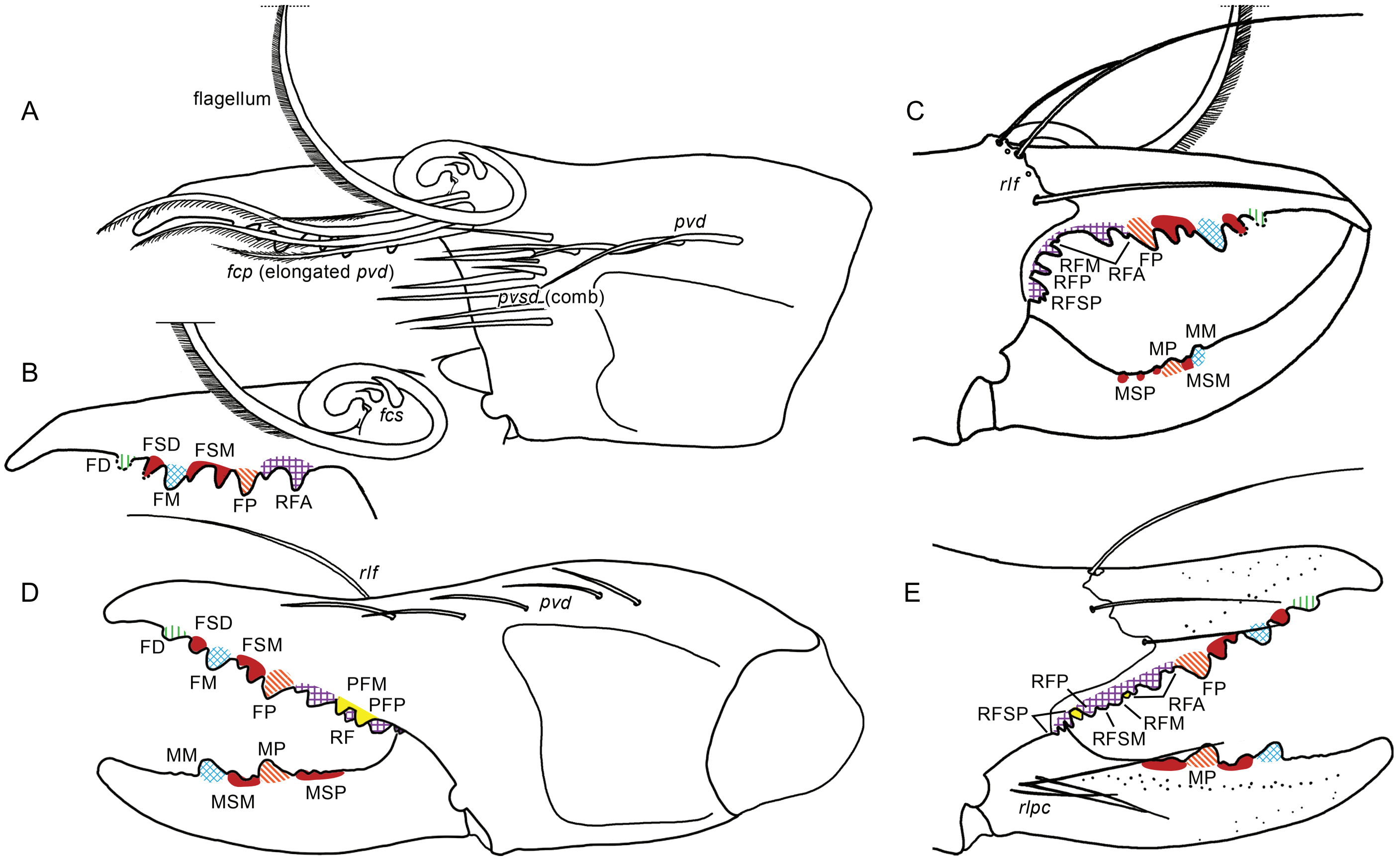

A
flagellum
fcp (elongated pvd)
pvd
pvsd (comb)
B
fcs
FD
FSD
FSM
FM
FP
RFA
C
rlf
RFM
RFP
RFSP
RFA
FP
MM
MP
MSM
MSP
D
rlf
pvd
FSD
FD
FSM
FM
FP
PFM
PFP
RF
MM
MP
MSM
MSP
E
RFP
RFSP
FP
RFA
RFM
RFSM
MP
rlpc

PLATE 51. Karschiidae Kraepelin, 1899, *Karschia* (*K.*) *mastigofera* Birula, 1890, chelicerae, prolateral (**A, D**) and retrolateral (**C, E**) views illustrating dentition, setae, and flagellar complex, and fixed finger, prolateral view, with *pvd* setae not shown to expose dentition (**B**). **A–C.** ♂ (AMNH [LP 7474]). **D, E.** ♀ (AMNH [LP 7476]). Abbreviations: ***fcp*****,** flagellar complex plumose setae; ***fcs*****,** flagellar complex subspiniform setae; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **MSP,** movable finger, subproximal teeth; ***pdp*****,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; ***pvd*****,** proventral distal setae; ***pvp*****,** proventral proximal setae; ***pvsd*****,** proventral subdistal setae (setal comb only); **RF,** retrofonal teeth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal teeth; **RFSM,** retrofondal submedial tooth; ***rlf*****,** retrolateral finger setae; ***rlpc*****,** retrolateral proximal setal cluster.

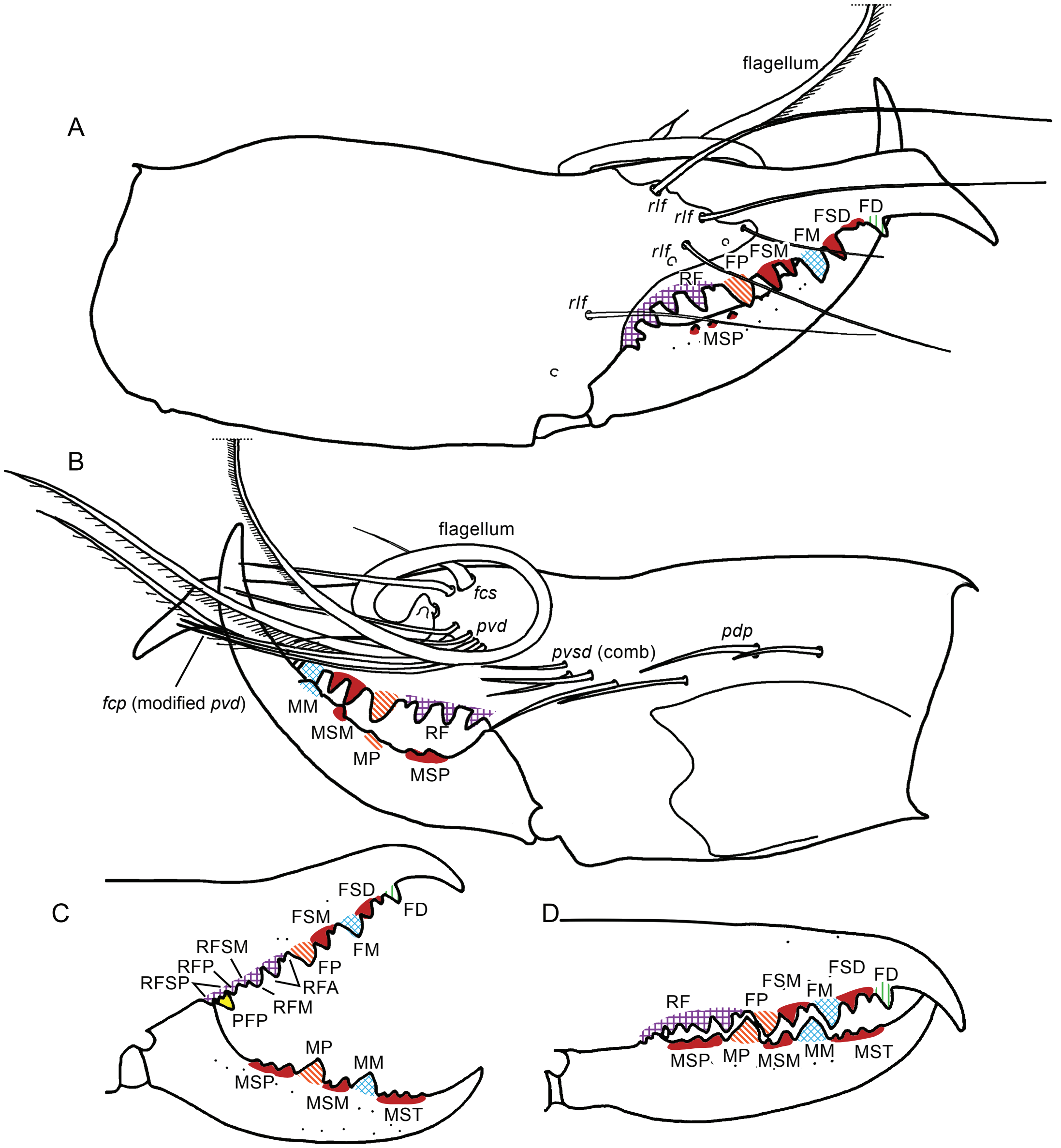

A
flagellum
rlf
rlf
FSD
FD
FM
rlf
FSM
FP
RF
rlf
MSP
B
flagellum
fcs
pvd
pvsd (comb)
pdp
fcp (modified pvd)
MM
MSM
RF
MP
MSP
C
FSD
FD
FSM
FM
RFSM
RFP
FP
RFSP
RFA
RFM
PFP
MP
MM
MSP
MSM
MST
D
FSD
FD
FSM
FM
RF
FP
MSP
MP
MSM
MM
MST

PLATE 52. Karschiidae Kraepelin, 1899, chelicerae, retrolateral (**A, C, D**) and prolateral (**B**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **C, D.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]), with cheliceral fingers open (**C**), and closed (**D**). Abbreviations: ***fcp*,** flagellar complex plumose setae; ***fcs*,** flagellar complex subspiniform setae; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **MSP,** movable finger, subproximal teeth; **MST,** movable finger, subterminal teeth; ***pdp*,** prodorsal proximal setae; **PFP,** profondal proximal teeth; ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal teeth; ***rlf*,** retrolateral finger setae.

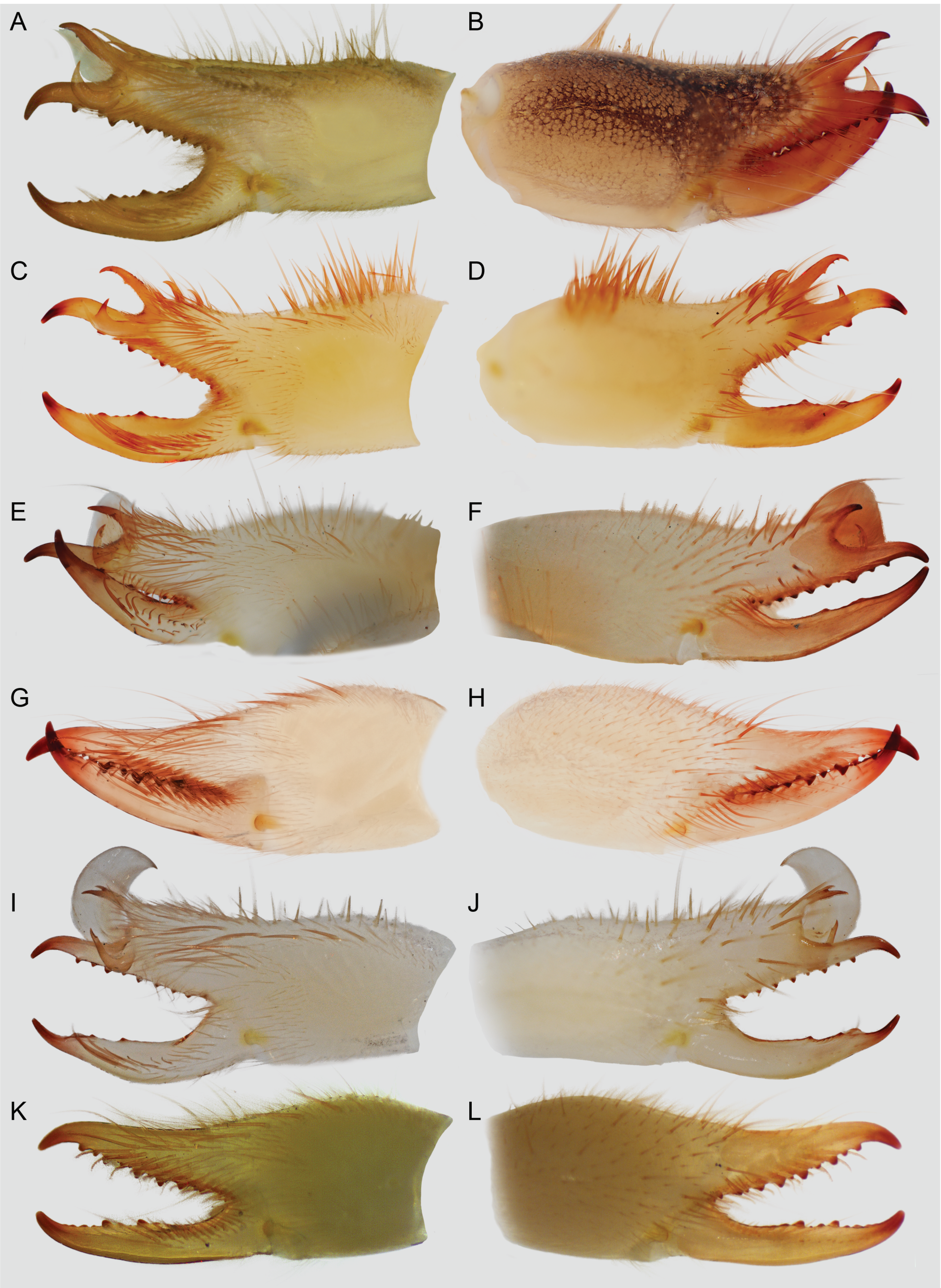


PLATE 53. Karschiidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I, K**) and retrolateral (**B, D, F, H, J, L**) views. **A, B.** *Eusimonia nigrescens* Kraepelin, 1899, ♂ (AMNH [LP 7473]). **C, D.** *Eusimonia furcillata* (Simon, 1872), ♂ (HUJI 769). **E–H.** *Eusimonia turkestana* Kraepelin, 1899. **E, F.** ♂ (AMNH [LP 4096]). **G, H.** ♀ (AMNH [LP 4097]). **I–L.** *Eusimonia divina* Birula, 1935. **I, J.** ♂ (AMNH [LP 4098]). **K, L** ♀ (AMNH [LP 4098]).

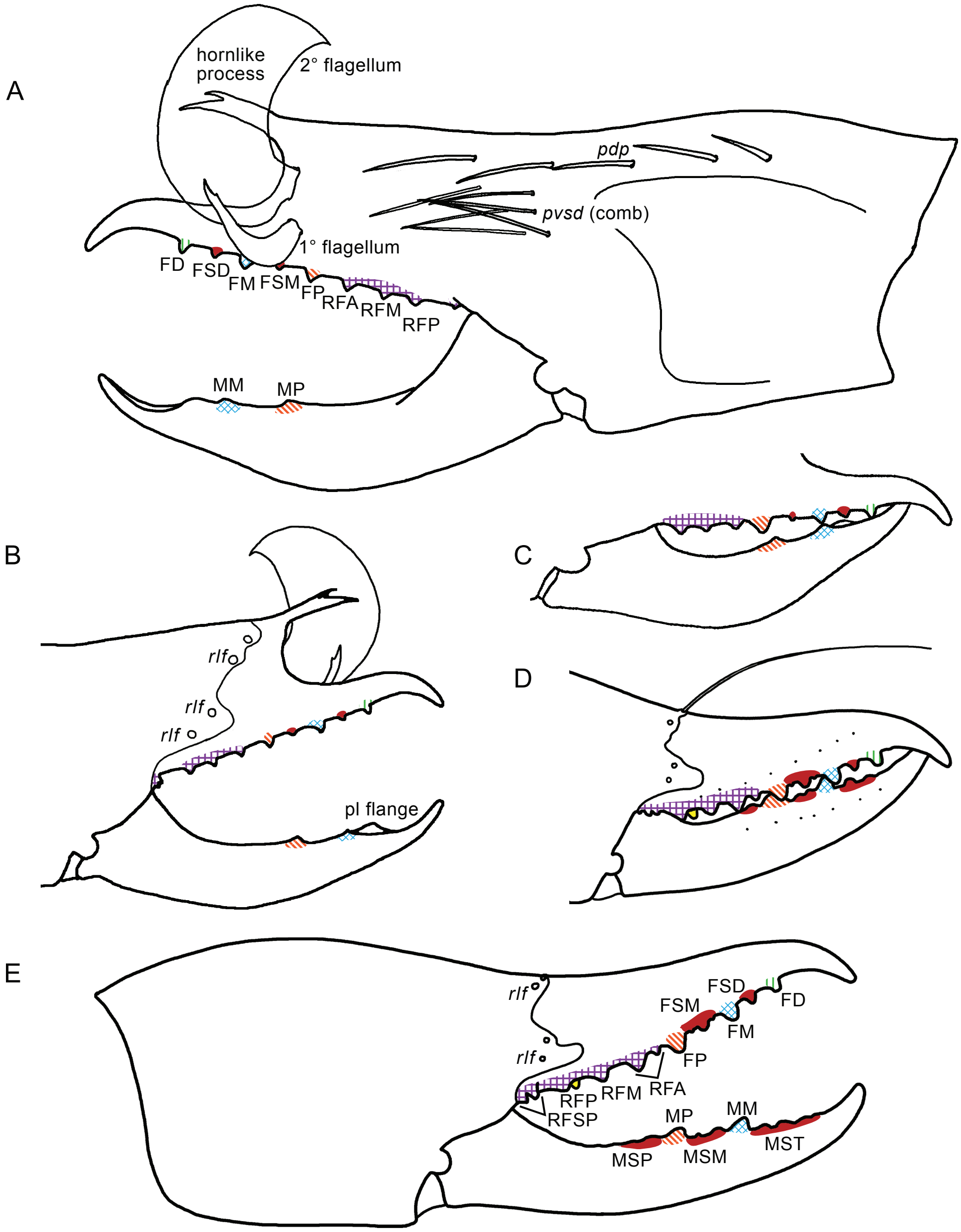

A
hornlike process
2° flagellum
pdp
pvsd (comb)
1° flagellum
FD
FSD
FM
FSM
FP
RFA
RFM
RFP
MM
MP
B
rlf
rlf
rlf
pl flange
C
D
E
rlf
rlf
FSD
FD
FSM
FM
FP
RFA
RFM
RFP
RFSP
MP
MM
MST
MSP
MSM

PLATE 54. Karschiidae Kraepelin, 1899, *Eusimonia divina* Birula, 1935, chelicerae, prolateral (**A**) and retrolateral (**B–E**) views, illustrating dentition, setae, and flagellar complex. **A–C.** ♂ (AMNH [LP 4098]). **D, E.** ♀ (AMNH [LP 4098]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM**, fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **MSP,** movable finger, subproximal teeth; **MST,** movable finger, subterminal teeth; ***pdp*,** prodorsal proximal setae; ***pvsd*,** proventral subdistal setae (setal comb only); ***pl*,** prolateral; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP**, retrofondal subproximal teeth; ***rlf*,** retrolateral finger setae; **1°,** primary; **2°,** secondary.

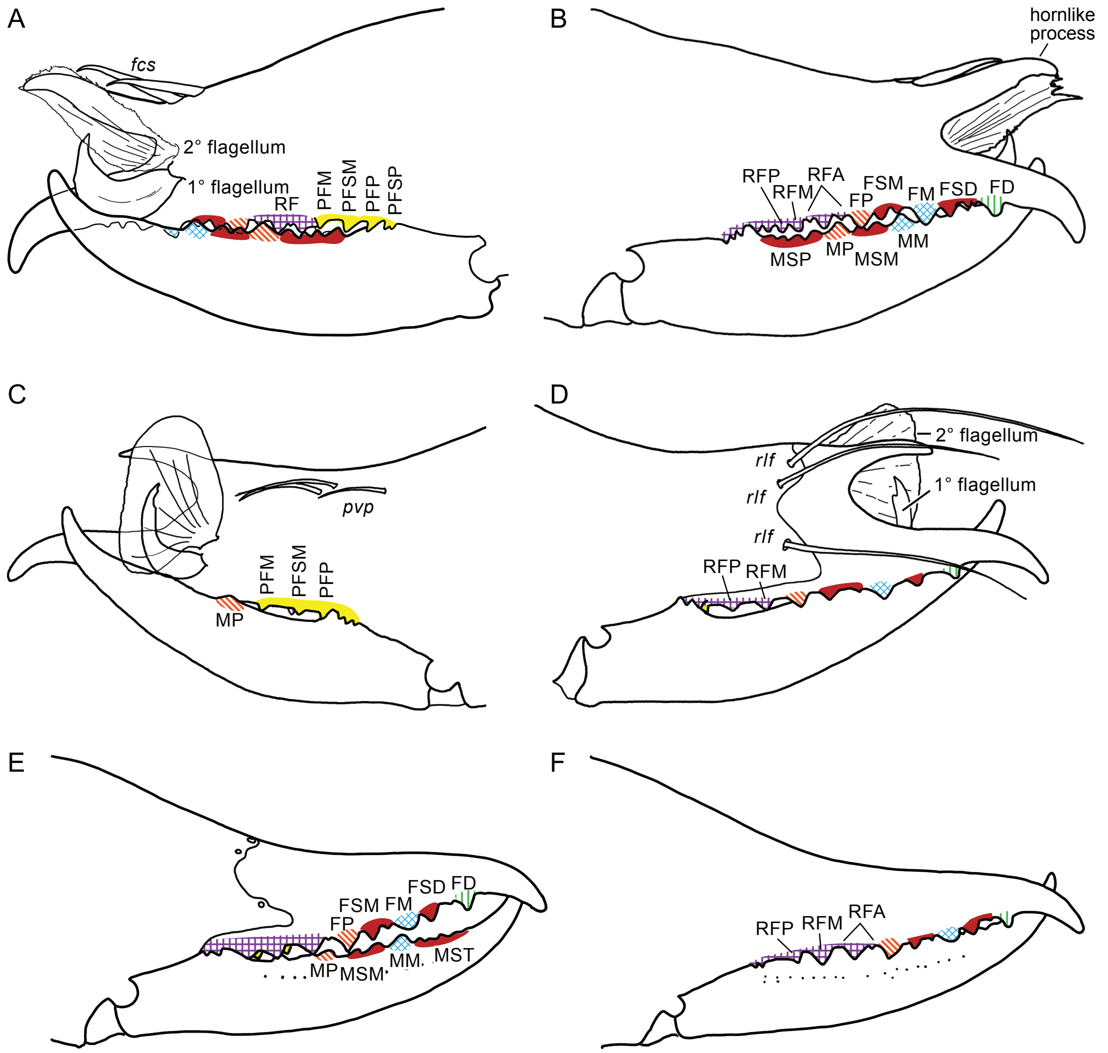

A
fcs
2° flagellum
1° flagellum
RF
PFM
PFSM
PFP
PFSP
B
hornlike process
RFP
RFA
RFM
FP
FSM
FM
FSD
FD
MSP
MP
MSM
MM
C
pvp
PFM
PFSM
PFP
MP
D
2° flagellum
rlf
rlf
1° flagellum
rlf
RFP
RFM
E
FSD
FD
FSM
FM
FP
MP
MSM
MM
MST
F
RFP
RFM
RFA

PLATE 55. Karschiidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B, D–F**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Eusimonia nigrescens* Kraepelin, 1899, ♂ (AMNH [LP 7473]). **C–F.** *Eusimonia turkestana* Kraepelin, 1899. **C, D.** ♂ (AMNH [LP 4096]). **E, F.** ♀ (AMNH [LP 4097]). Abbreviations: ***fcs*,** flagellar complex subspiniform setae; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **MST,** movable finger, subterminal teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvp*,** proventral proximal setae; **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; ***rlf*,** retrolateral finger setae; **1°,** primary; **2°,** secondary.

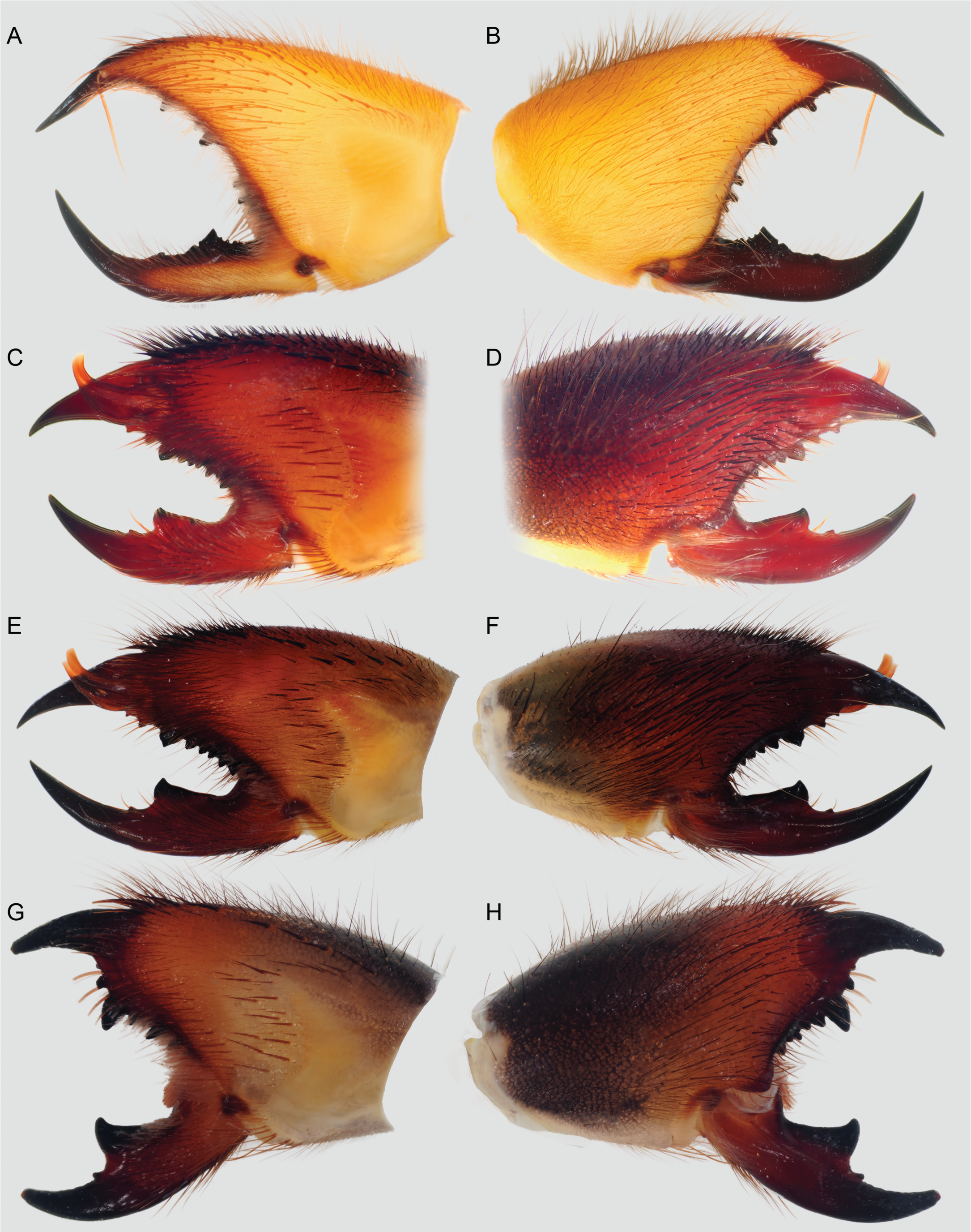


PLATE 56. Dinorhaxinae Roewer, 1933 (**A, B**) and Rhagodidae, Pocock, 1897 (**C–H**), chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **C, D.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). **E–H.** *Rhagodes melanus* (Olivier, 1807). **E, F.** ♂ (AMNH [LP 2293]). **G, H.** ♀ (AMNH [LP 10549]).

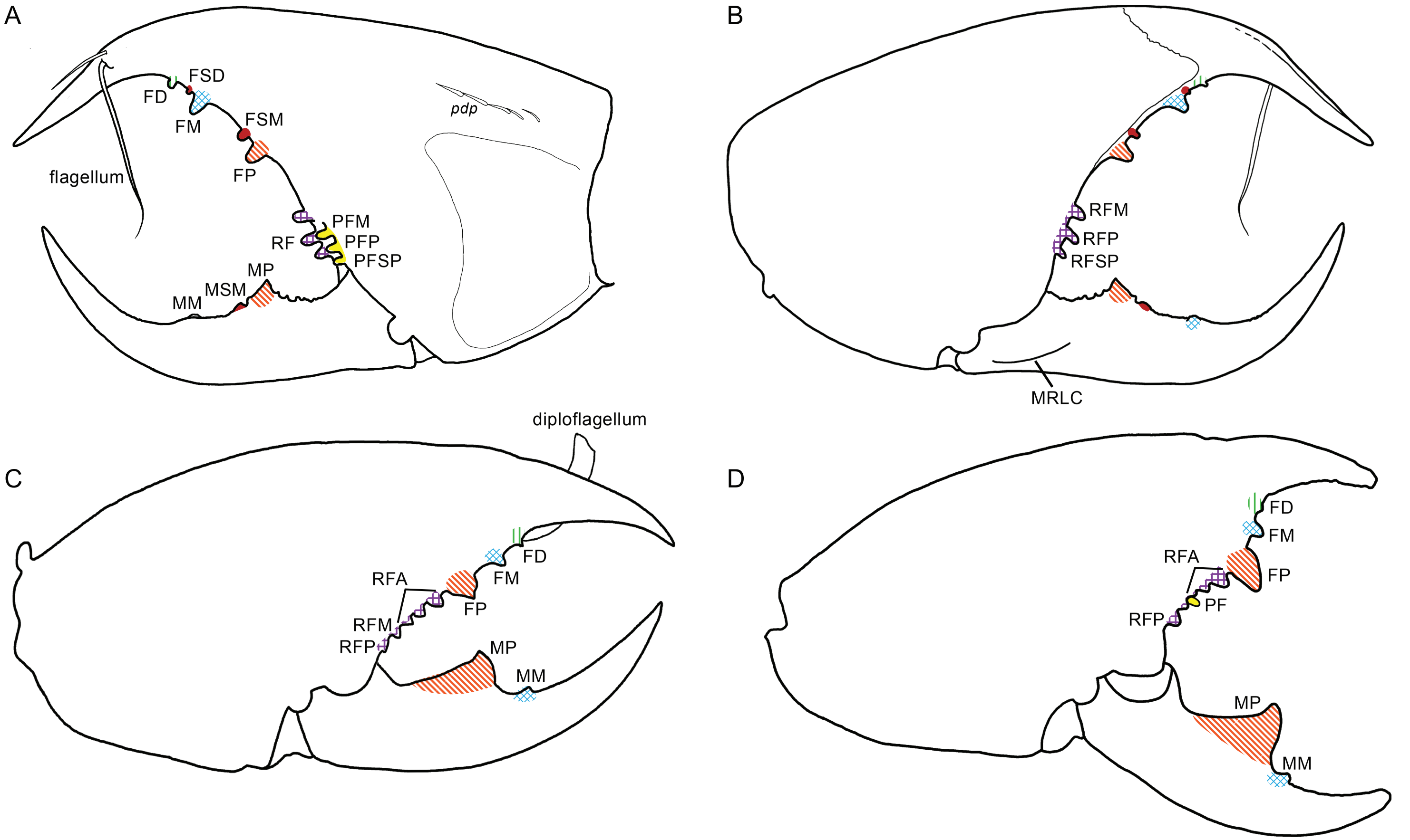

A
FD
FSD
FM
FSM
FP
flagellum
pdp
PFM
RF
PFP
PFSP
MP
MSM
MM
B
RFM
RFP
RFSP
MRLC
C
diploflagellum
FD
FM
RFA
FP
RFM
RFP
MP
MM
D
FD
FM
RFA
FP
PF
RFP
MP
MM

PLATE 57. Dinorhaxinae Roewer, 1933 (**A, B**) and Rhagodidae Pocock, 1897 (**C, D**), chelicerae, prolateral (**A**) and retrolateral (**B–D**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **C, D.** *Rhagodes melanus* (Olivier, 1807). **C.** ♂ (AMNH [LP 2293]). **D.** ♀ (AMNH [LP 10549]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **MP,** movable finger, proximal tooth; **MM,** movable finger, medial tooth; **MRLC,** movable finger, retrolateral carina; **MSM,** movable finger, submedial tooth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PF,** profondal teeth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal teeth.

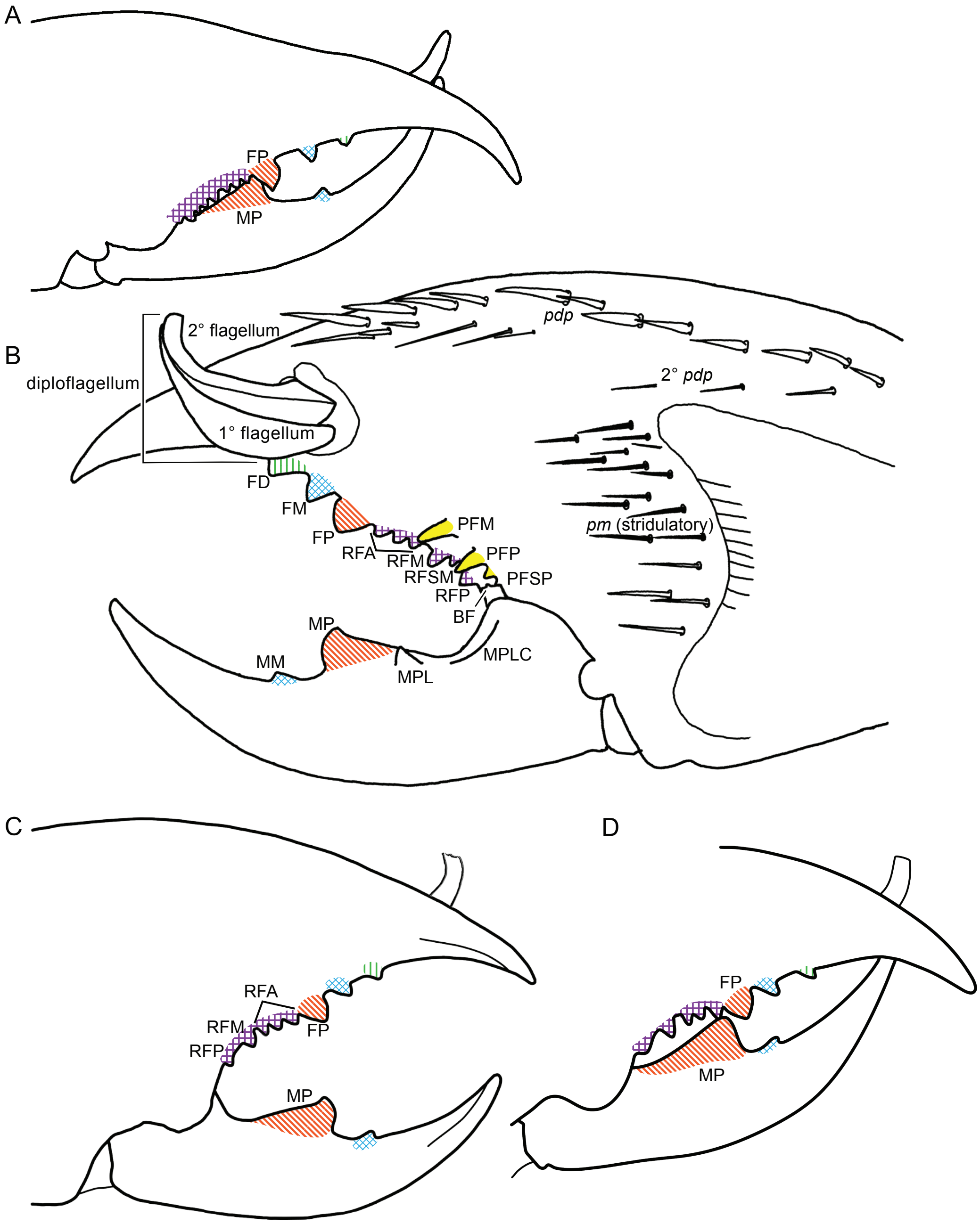

A
FP
MP
B
2° flagellum
diploflagellum
1° flagellum
pdp
2° *pdp*
FD
FM
FP
PFM
RFA
RFM
PFP
RFSM
PFSP
RFP
BF
pm (stridulatory)
MP
MM
MPL
MPLC
C
RFA
RFM
RFP
FP
MP
D
FP
MP

PLATE 58. Rhagodidae, Pocock, 1897, chelicerae, retrolateral (**A, C, D**) and prolateral (**B**) views, illustrating dentition, setae, and flagellar complex. **A.** Indet. ♂ (MCZ 126321). **B–D.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). Abbreviations: **BF,** basifondal teeth; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MPLC,** movable finger, prolateral carina; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **pl,** prolateral; ***pm*,** promedial setae; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial teeth; **1°,** primary; **2°,** secondary.

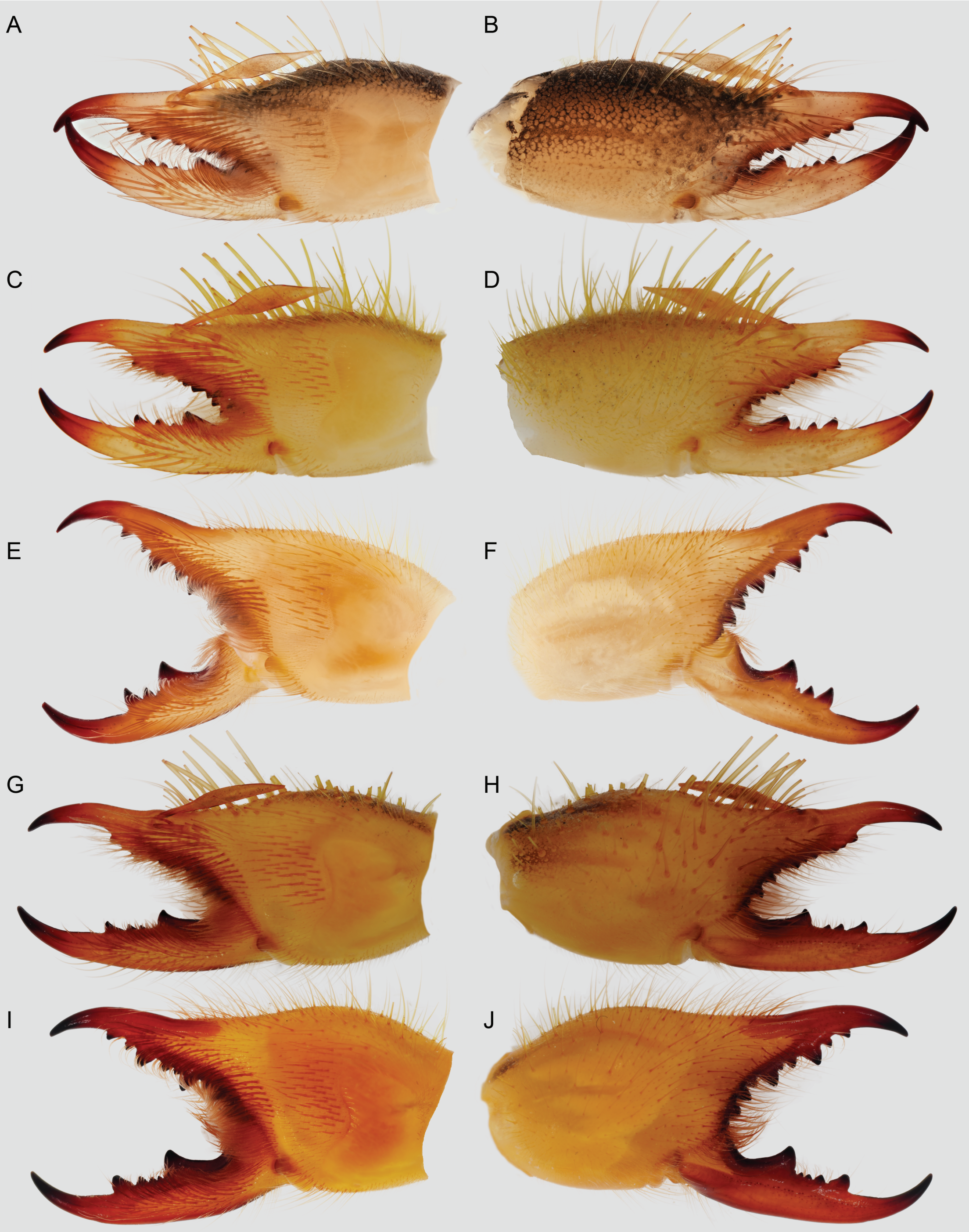


PLATE 59. Galeodidae Sundevall, 1833, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Paragaleodes nesterovi* Birula, 1916, ♂ (AMNH [LP 7480]). **C, D.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]). **E, F.** *Paragaleodes* sp., ♀ (AMNH [LP 10550]). **G–J.** *Galeodes araneoides* (Pallas, 1772). **G, H.** ♂ (AMNH), Turkey: Gurgen. **I–J.** ♀ (AMNH), Turkey: Gurgen.

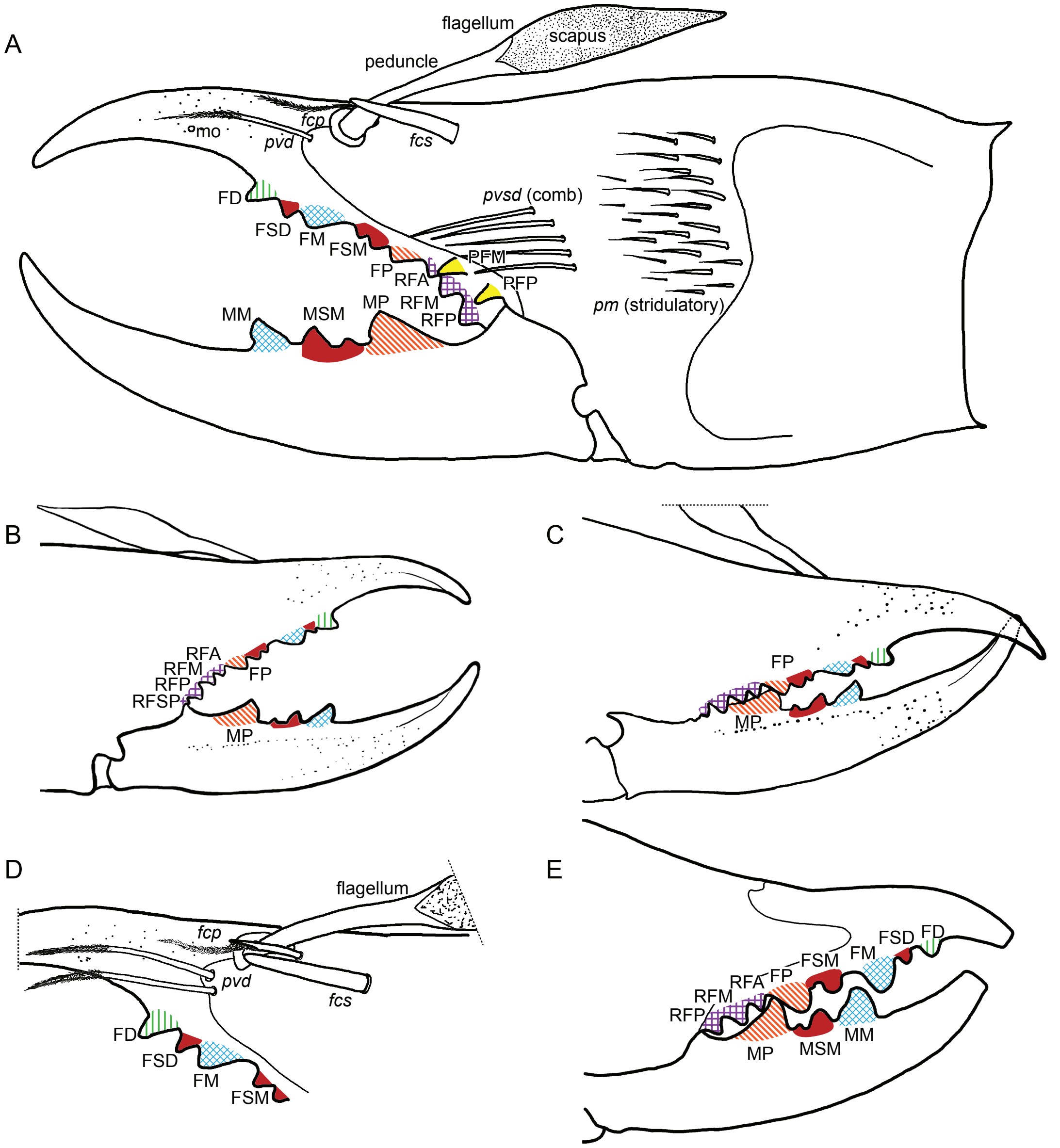

A
flagellum
scapus
peduncle
fcp
mo
pvd
fcs
pvsd (comb)
FD
FSD
FM
FSM
FP
RFA
PFM
PFP
MP
RFM
RFP
MM
MSM
pm (stridulatory)
B
RFA
RFM
RFP
RFSP
FP
MP
C
FP
MP
D
flagellum
fcp
pvd
fcs
FD
FSD
FM
FSM
E
FSD
FD
FM
FSM
RFA
FP
RFM
RFP
MP
MSM
MM

PLATE 60. Galeodidae Sundevall, 1833, chelicerae, prolateral (**A**), and retrolateral (**B, C, E**) views, and fixed finger, prolateral view (**D**), illustrating dentition, setae, and flagellar complex. **A–D.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]) with abnormal *fcp* seta (spinose proximally and plumose distally). **E.** *Galeodes* sp., ♀ (MCZ), Niger: Birni N'kare. Abbreviations: ***fcp*,** flagellar complex plumose setae; ***fcs*,** flagellar complex spiniform seta; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **mo,** mucron organ; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; ***pm*,** promedial setae (only stridulatory setae shown); ***pvd*,** proventral distal setae (only one or two apicalmost setae shown); ***pvsd*,** proventral subdistal setae (setal comb only); **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal teeth.

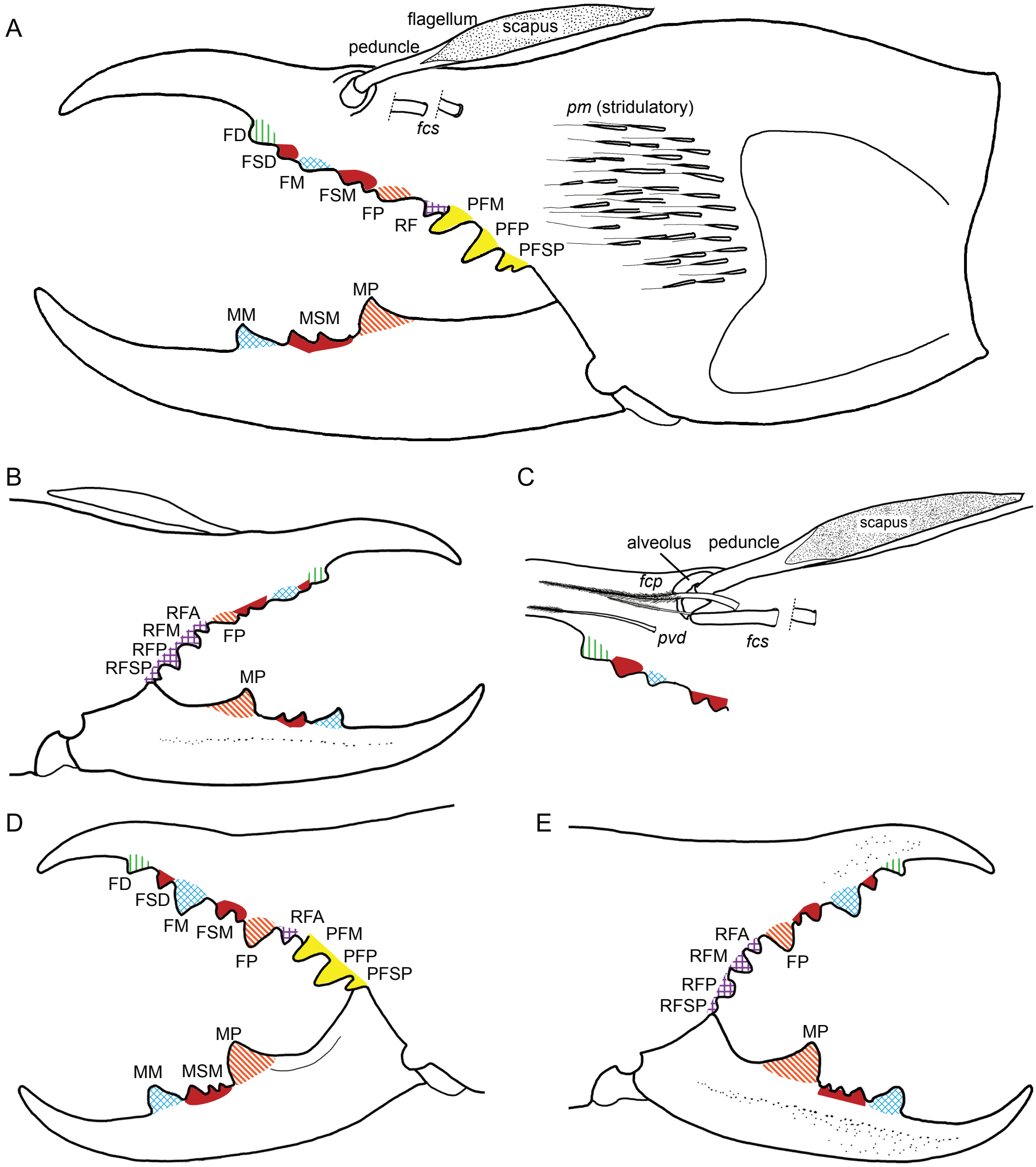

A
flagellum
scapus
peduncle
fcs
pm (stridulatory)
FD
FSD
FM
FSM
FP
RF
PFM
PFP
PFSP
MP
MM
MSM
B
RFA
RFM
RFP
RFSP
FP
MP
C
alveolus
peduncle
scapus
fcp
pvd
fcs
D
FD
FSD
FM
FSM
FP
RFA
PFM
PFP
PFSP
MP
MM
MSM
E
RFA
RFM
RFP
RFSP
FP
MP

PLATE 61. Galeodidae Sundevall, 1833, *Galeodes araneoides* (Pallas, 1772), chelicerae, prolateral (**A, D**), and retrolateral (**B, E**) views, and fixed finger, prolateral view (**C**), illustrating dentition, setae, and flagellar complex. **A–C.** ♂ (AMNH), Turkey: Gurgen. **D, E.** ♀ (AMNH), Turkey: Gurgen. Abbreviations: ***fcp*****,** flagellar complex plumose seta; ***fcs*****,** flagellar complex spiniform setae; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pm*****,** promedial setae (only stridulatory setae shown); ***pvd*****,** proventral distal setae (only apicalmost seta shown); **RF,** retrofondal teeth; **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth.

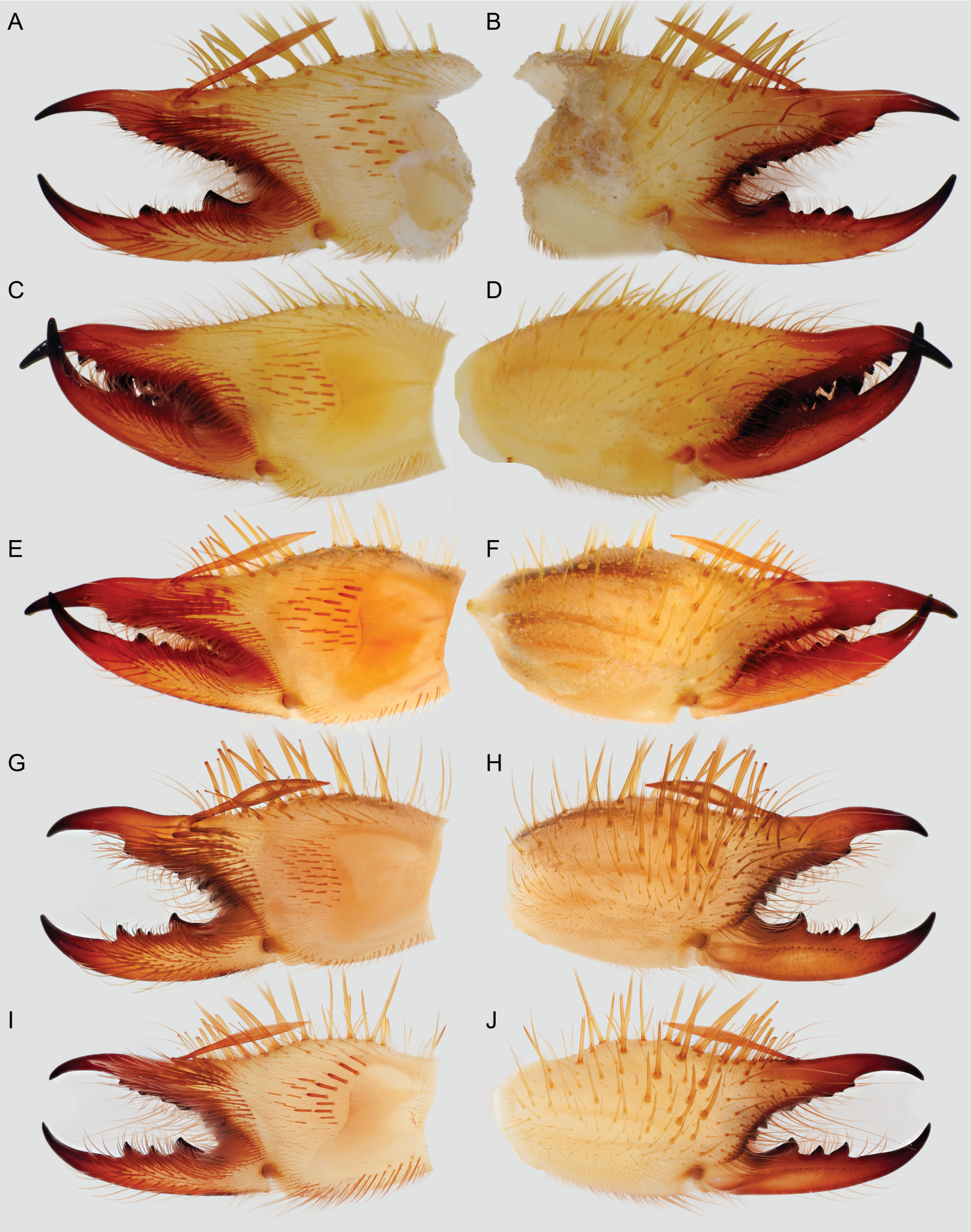


PLATE 62. Galeodidae Sundevall, 1833, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Galeodes olivieri* Simon 1879. **A, B.** ♂ (AMNH [LP 4630]). **C, D.** ♀ (AMNH [LP 4628]). **E, F.** *Galeodes arabs* C.L. Koch, 1842, ♂ (AMNH [LP 9123]). **G, H.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 7536]). **I, J.** *Galeodes* sp., ♂ (AMNH [LP 11204]).

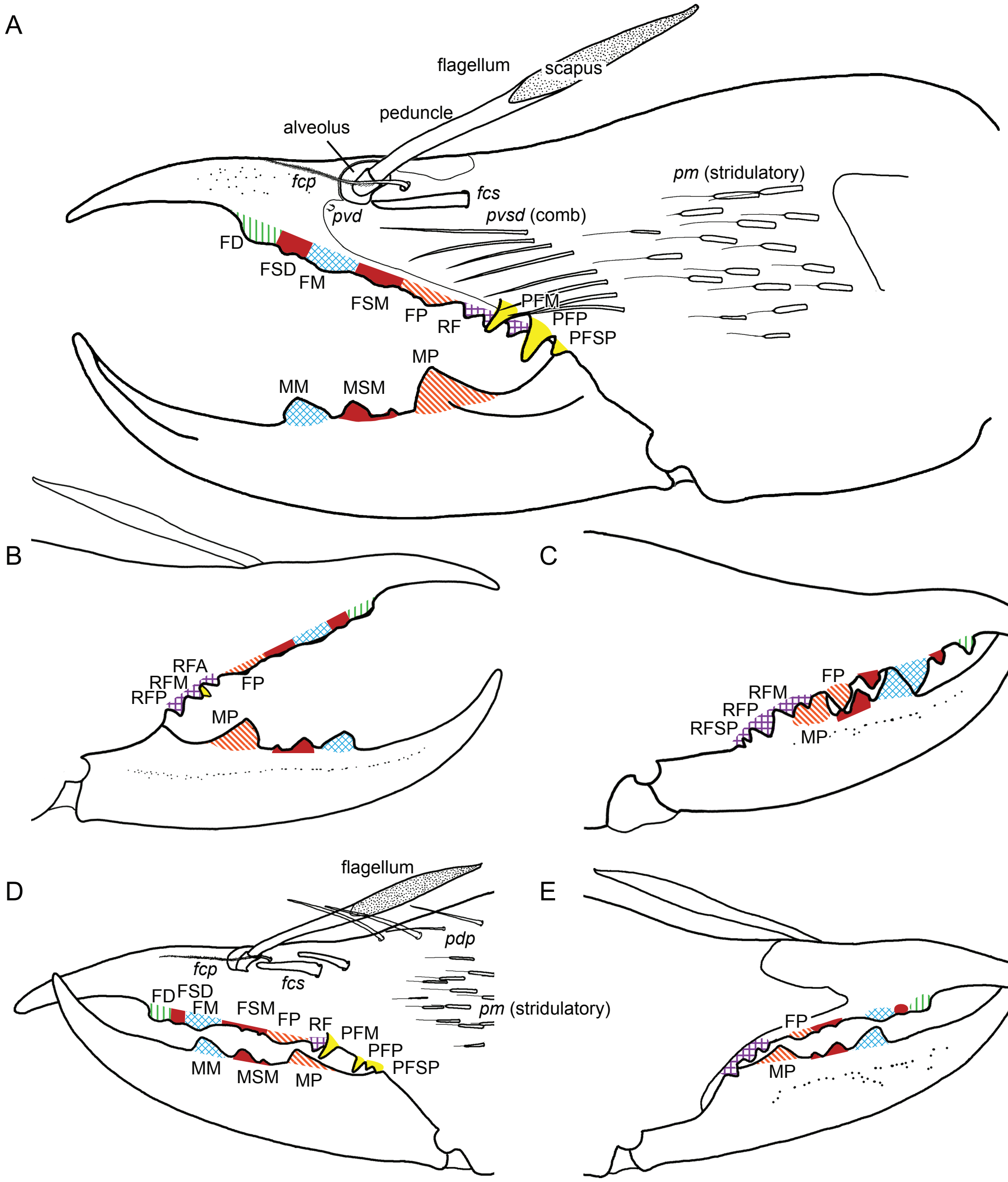

A
flagellum
scapus
peduncle
alveolus
fcp
fcs
pm (stridulatory)
pvd
pvsd (comb)
FD
FSD
FM
FSM
FP
RF
PFM
PFP
PFSP
MP
MM
MSM
B
RFA
RFM
RFP
FP
MP
C
FP
RFM
RFP
RFSP
MP
D
flagellum
pdp
fcp
fcs
pm (stridulatory)
FD
FSD
FM
FSM
FP
RF
PFM
PFP
PFSP
MM
MSM
MP
E
FP
MP

PLATE 63. Galeodidae Sundevall, 1833, chelicerae, prolateral (**A, D**) and retrolateral (**B, C, E**) views, illustrating dentition, setae, and flagellar complex. **A–C.** *Galeodes olivieri* Simon 1879. **A, B.** ♂ (AMNH [LP 4630]). **C.** ♀ (AMNH [LP 4628]). **D, E.** *Galeodes arabs* C.L. Koch, 1842, ♂ (AMNH [LP 9123]). Abbreviations: ***fcp*,** flagellar complex plumose setae; ***fcs*,** flagellar complex spiniform setae; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pm*,** promedial setae (only stridulatory setae shown); ***pvd*,** proventral distal seta (socket only); ***pvsd*,** profondal subdistal (setal comb only); **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal teeth.

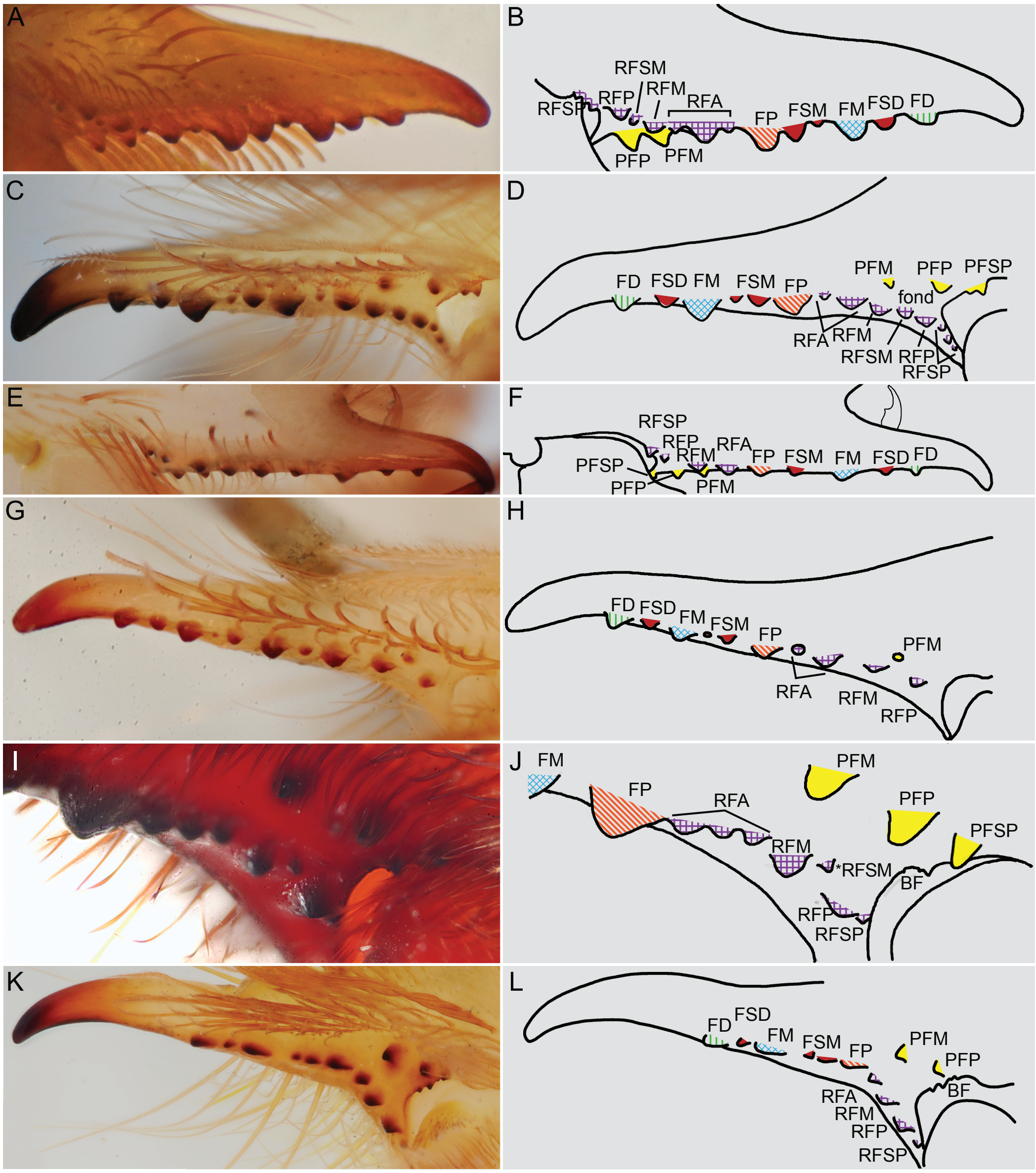

A
B
RFSM
RFP
RFM
RFA
RFSP
FP
FSM
FM
FSD
FD
PFP
PFM
C
D
FD
FSD
FM
FSM
FP
PFM
PFP
PFSP
fond
RFA
RFM
RFSM
RFP
RFSP
E
F
RFSP
RFP
RFM
RFA
FP
FSM
FM
FSD
FD
PFSP
PFP
PFM
G
H
FD
FSD
FM
FSM
FP
PFM
RFA
RFM
RFP
I
J
FM
FP
RFA
PFM
PFP
PFSP
RFM
*RFSM
BF
RFP
RFSP
K
L
FD
FSD
FM
FSM
FP
PFM
PFP
BF
RFA
RFM
RFP
RFSP

PLATE 64. Karschiidae Kraepelin, 1899 (**A–H**), Rhagodidae Pocock, 1897 (**I, J**), and Galeodidae Sundevall, 1833 (**K, L**), cheliceral fixed fingers, retroventral (**A, B, E, F**) and proventral (**C, D, G–L**) views illustrating fondal area and basifondal teeth (**I–L**). **A, B.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♀ (AMNH [LP 7476]). **C, D** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **E, F.** *Eusimonia turkestana* Kraepelin, 1899, ♂ (AMNH [LP 4096]). **G, H.** *Eusimonia divina* Birula, 1935, ♀ (AMNH [LP 4098]). **I, J.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). **K, L.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]). Asterisk (**J**) indicates tooth not visible in retrolateral view. Abbreviations: **BF,** basifondal teeth; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal teeth.

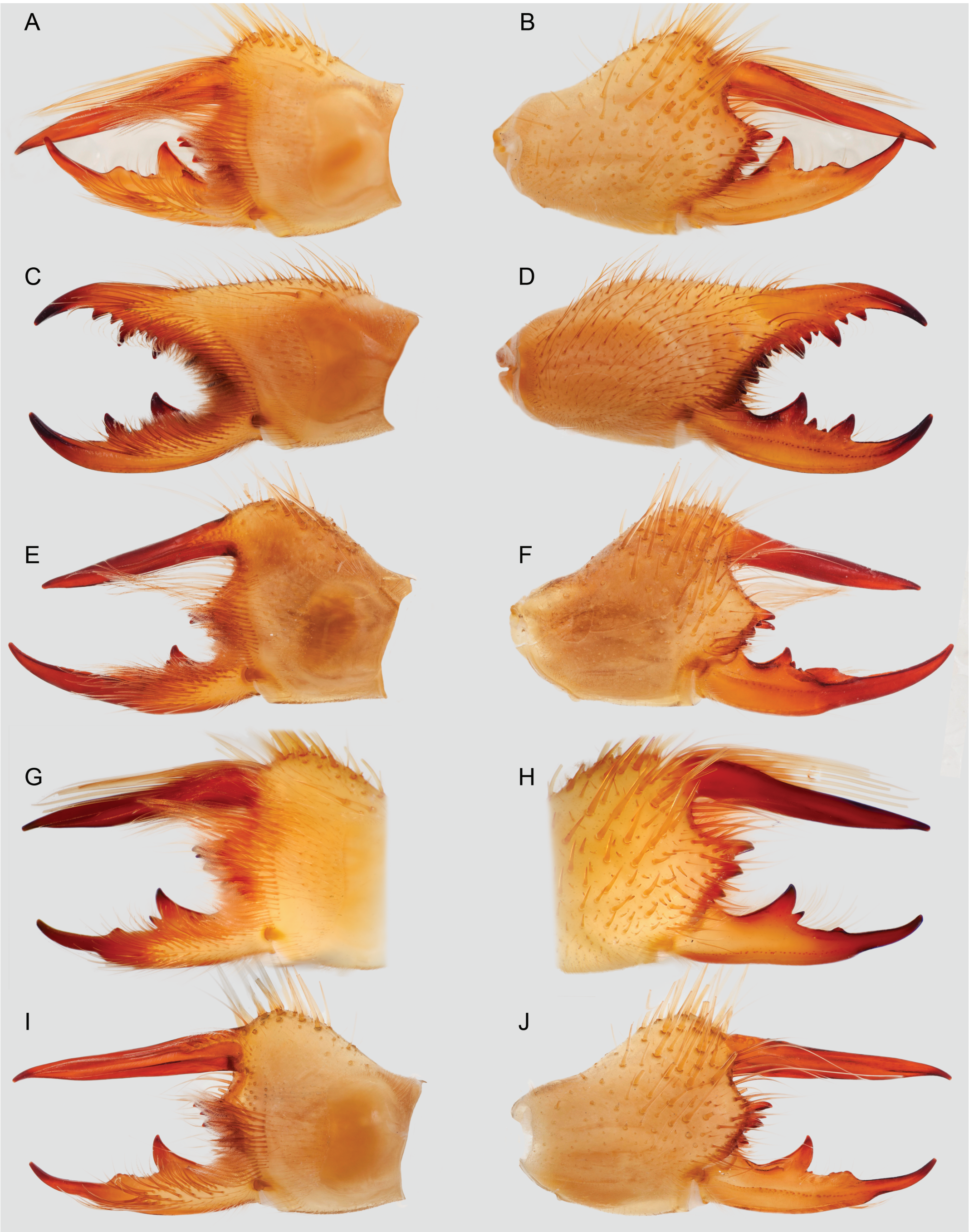


PLATE 65. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Eremobates ajoanus* Muma and Brookhart, 1988. **A, B.** Paratype ♂ (DMNS ZA.17384). **C, D.** Paratype ♀ (DMNS ZA.17311). **E, F.** *Eremobates angustus* Muma, 1951, paratype ♂ (DMNS ZA.16789). **G, H.** *Eremobates bajadae* Muma and Brookhart, 1988, ♂ (AMNH [LP 5740]). **I, J.** *Eremobates bixleri* Muma and Brookhart, 1988, paratype ♂ (DMNS ZA.17386).

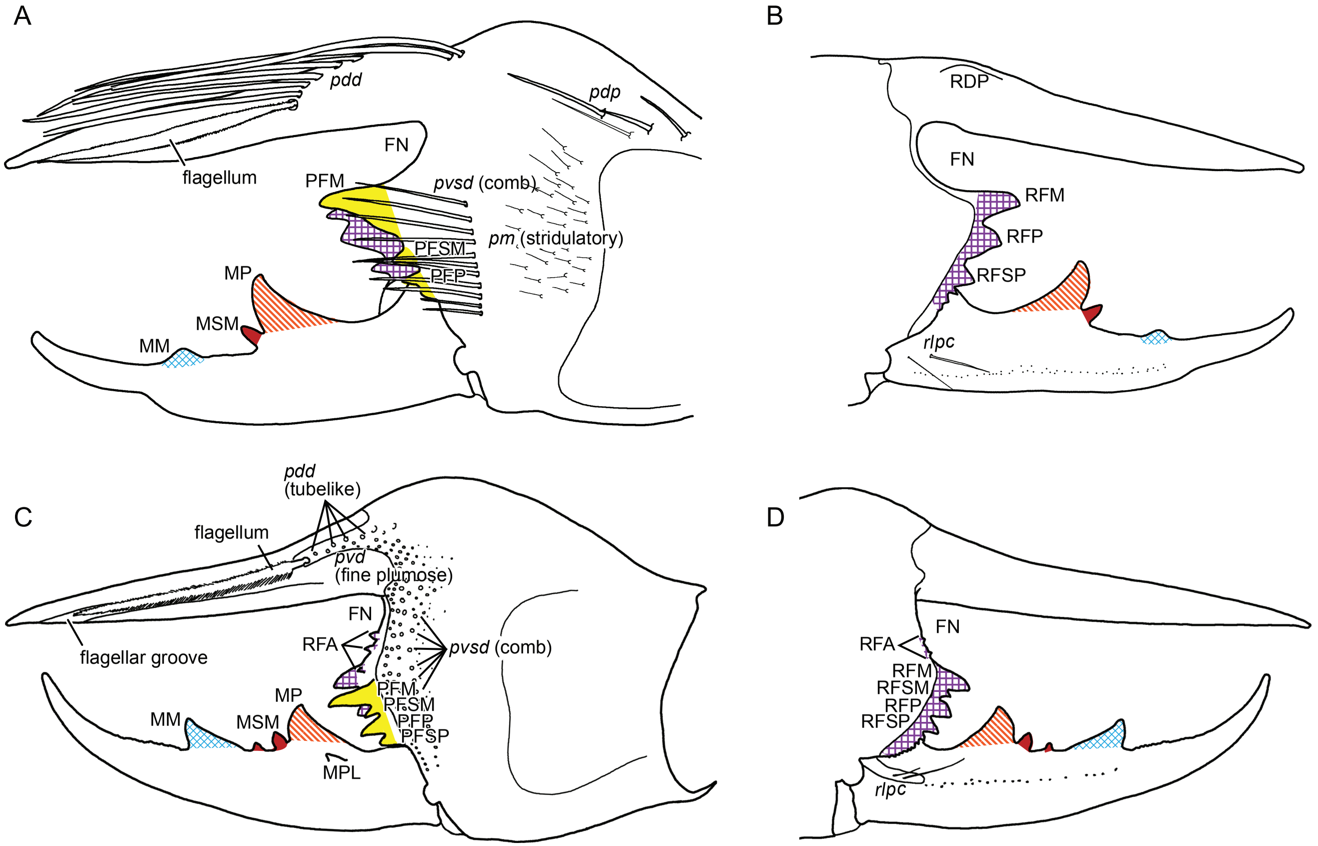

A
pdd
pdp
flagellum
FN
PFM
pvsd (comb)
pm (stridulatory)
PFSM
PFP
MP
MSM
MM
B
RDP
FN
RFM
RFP
RFSP
rlpc
C
pdd
(tubelike)
flagellum
pvd
(fine plumose)
FN
RFA
pvsd (comb)
flagellar groove
MP
MM
MSM
PFM
PFSM
PFP
PFSP
MPL
D
FN
RFA
RFM
RFSM
RFP
RFSP
rlpc

PLATE 66. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). **A, B.** *Eremobates bajadae* Muma and Brookhart, 1988, ♂ (AMNH [LP 5740]). **C, D.** *Eremobates gerbae* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10000). Abbreviations: **FN,** fondal notch; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MSM,** movable finger, submedial teeth; ***pdd*,** prodorsal distal setae; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pm*,** promedial setae (stridulatory setae only); ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae (including setal comb); **RDP,** retrodorsal process; **RFA,** retrofondal apical teeth (denticles); **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

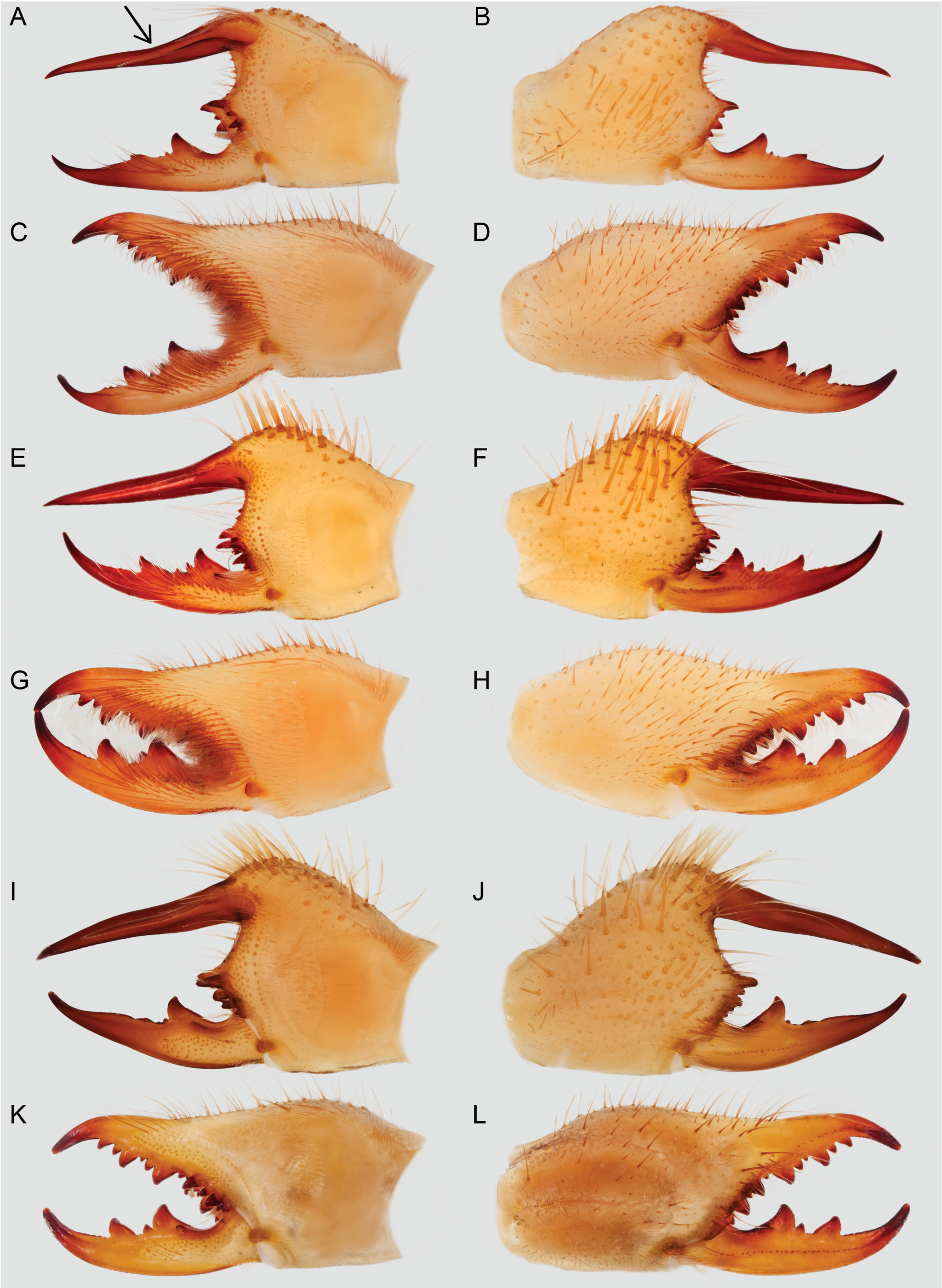


PLATE 67. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I, K**) and retrolateral (**B, D, F, H, J, L**) views. **A–D.** *Eremobates corpink* Brookhart and Cushing, 2004. **A, B.** Holotype ♂ (DMNS ZA.17380). Arrow (**A**) indicates fixed finger crimp. **C, D.** Paratype ♀ (DMNS ZA.17379). **E–H.** *Eremobates gerbae* Brookhart and Cushing, 2002. **E, F.** Holotype ♂ (DMNS ZA.10000). **G, H.** Paratype ♀ (DMNS ZA.10001). **I–L.** *Eremobates icenoglei* Brookhart and Cushing, 2004. **I, J.** Holotype ♂ (DMNS ZA.17376). **K, L.** Paratype ♀ (DMNS ZA.17377).

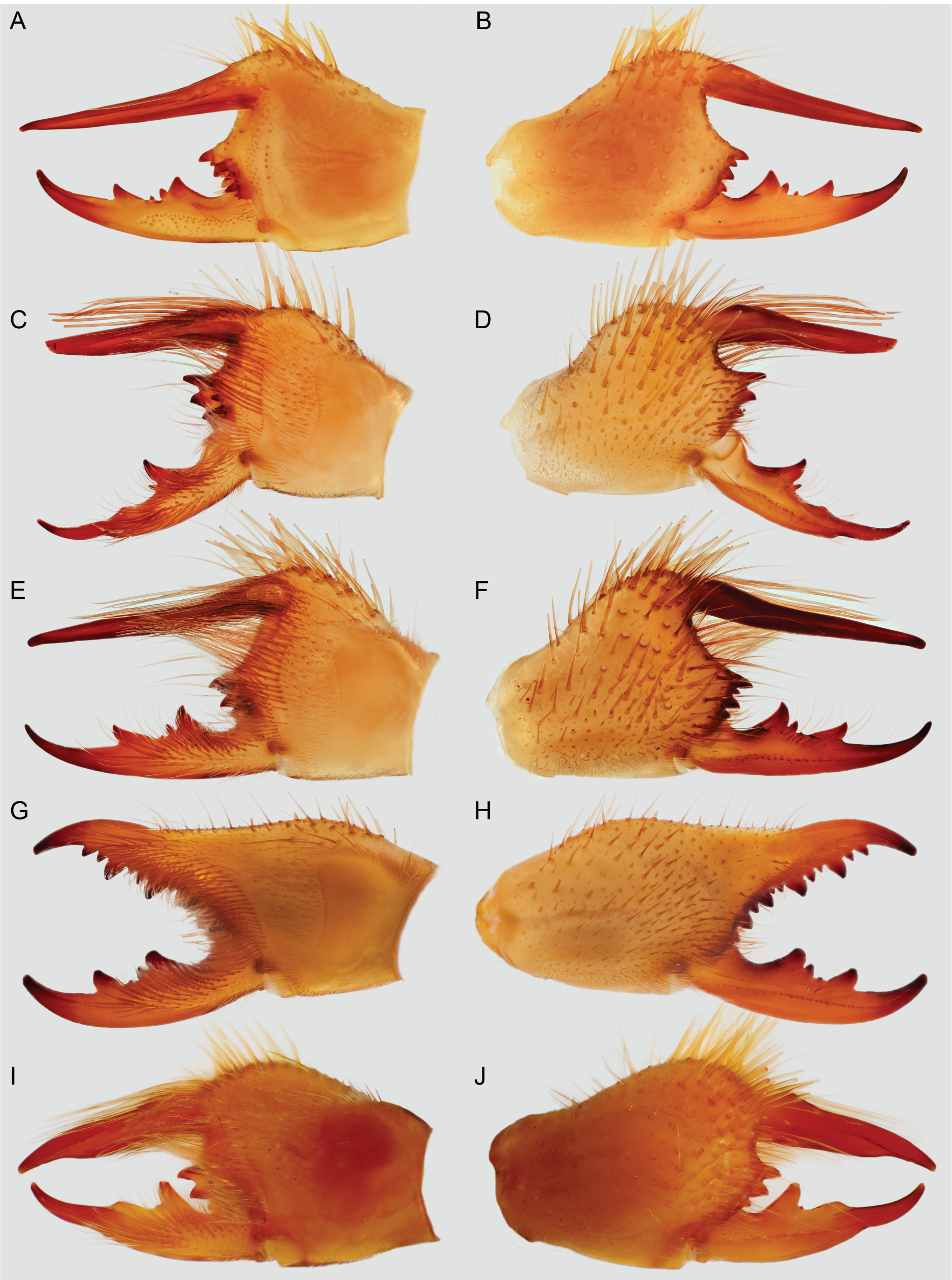


PLATE 68. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Eremobates chihuaensis* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10002). **C, D.** *Eremobates palpisetulosus* Fichter, 1941, ♂ (DMNS ZA.15683). **E–H.** *Eremobates pallipes* (Say, 1823). **E, F.** ♂ (DMNS ZA.16258). **G, H.** ♀ (DMNS ZA.15662). **I, J.** *Eremobatus tuberculatus* (Kraepelin, 1899), ♂ (AMNH), USA: Mokelumne Hill.

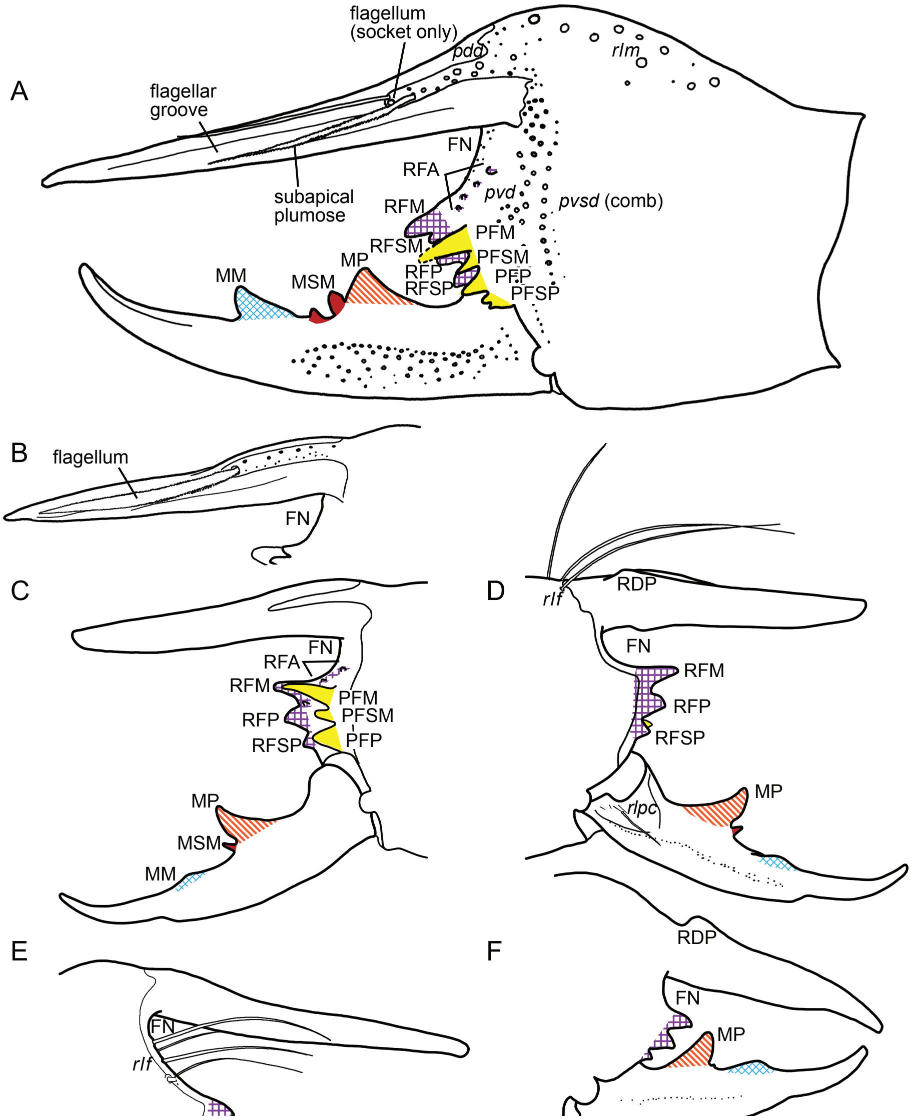

A
flagellum
(socket only)
pdd
rlm
flagellar
groove
FN
RFA
subapical
plumose
RFM
pvd
pvsd (comb)
PFM
RFSM
PFSM
MP
RFP
PFP
RFSP
PFSP
MM
MSM
B
flagellum
FN
C
FN
RFA
RFM
PFM
PFSM
RFP
PFP
RFSP
MP
MSM
MM
D
rlf
RDP
FN
RFM
RFP
RFSP
MP
rlpc
E
FN
rlf
F
RDP
FN
MP

PLATE 69. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**D, F**) views and fixed finger, prolateral (**B**) and retrolateral (**E**) views, illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). **A.** *Eremobates chihuaensis* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10002). **B.** *Eremobates* cf. *palpisetulosus*, ♂ (AMNH), Mexico: Coahuila, dorsal finger showing male flagellum (apical setae) and setal sockets. **C, D.** *Eremobates palpisetulosus* Fichter, 1941, ♂ (DMNS ZA.15683). **E.** *Eremobates pallipes* (Say, 1823), ♂ (DMNS ZA.16258), dorsal finger showing setae situated distally in fondal notch. **F.** *Eremobatus tuberculatus* (Kraepelin, 1899), ♂ (AMNH), USA: Mokelumne Hill. Abbreviations: **FN,** fondal notch; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; ***pdd*,** prodorsal distal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal teeth; ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae (including setal comb); **RDP,** retrodorsal process; **RFA,** retrofondal apical teeth (denticles); **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlf*,** retrolateral finger setae; ***rlpc*,** retrolateral proximal setal cluster; ***rlm*,** retrolateral manus setae.

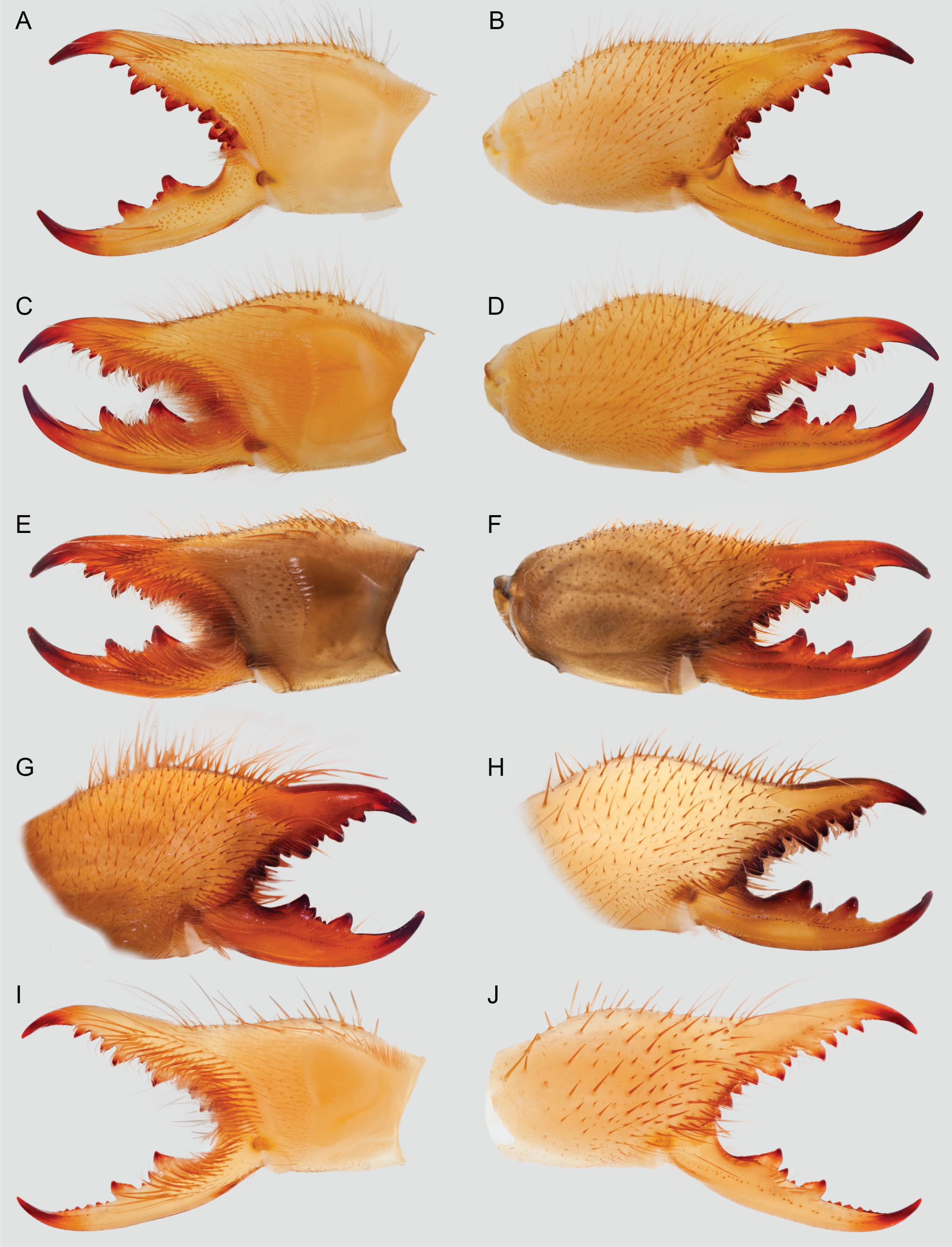


PLATE 70. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, I**) and retrolateral (**B, D, F–H, J**) views. **A, B.** *Eremobates polhemusi* Muma and Brookhart, 1988, ♀ (DMNS ZA.10004). **C, D.** *Eremobates inkopaensis* Brookhart and Cushing, 2005, paratype ♀ (DMNS ZA.17310). **E, F.** *Eremobates kiseri* Muma and Brookhart, 1988, paratype ♀ (DMNS ZA.17385). **G.** *Eremobates norrisi* Muma and Brookhart, 1988, paratype ♀ (DMNS ZA.17383). **H.** *Eremobates socal* Brookhart and Cushing, 2004, paratype ♀ (DMNS ZA.17378). **I, J.** *Horribates bantai* Muma, 1989, ♀ (DMNS ZA.17691).

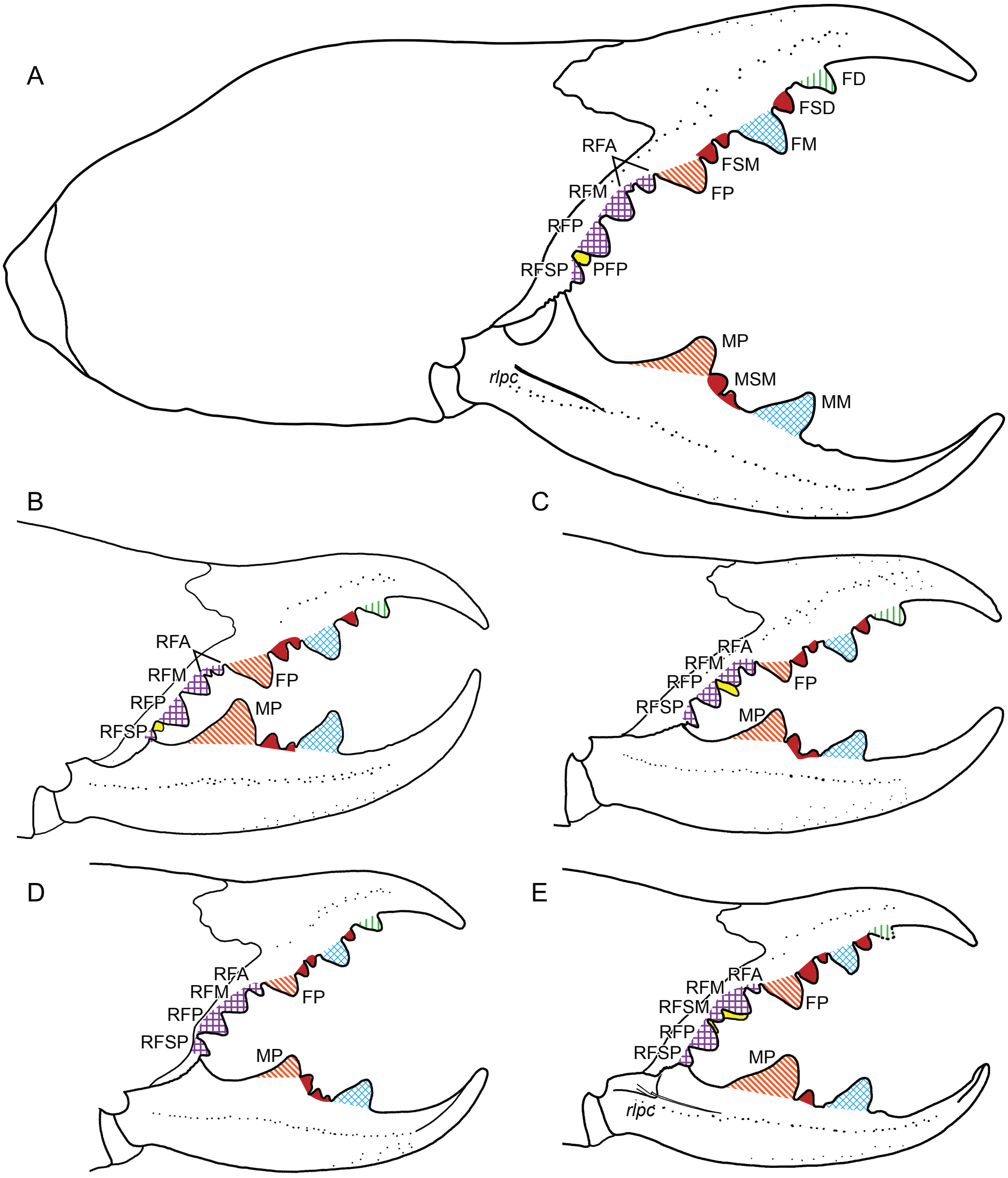

A
FD
FSD
FM
RFA
FSM
RFM
FP
RFP
RFSP
PFP
MP
rlpc
MSM
MM
B
RFA
RFM
FP
RFP
MP
RFSP
C
RFA
RFM
RFP
FP
RFSP
MP
D
RFA
RFM
FP
RFP
RFSP
MP
E
RFM
RFA
RFSM
FP
RFP
RFSP
MP
rlpc

PLATE 71. Eremobatidae Kraepelin, 1899, chelicerae, retrolateral views, illustrating dentition and setae. **A.** *Eremobates polhemusi* Muma and Brookhart, 1984, ♀ (DMNS ZA.10004). **B.** *Eremobates inkopaensis* Brookhart and Cushing, 2005, paratype ♀ (DMNS ZA.17310). **C.** *Eremobates kiseri* Muma and Brookhart, 1988, paratype ♀ (DMNS ZA.17385). **D.** *Eremobates norrisi* Muma and Brookhart, 1988, paratype ♀ (DMNS ZA.17383). **E.** *Eremobates socal* Brookhart and Cushing, 2004, paratype ♀ (DMNS ZA.17378). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **PFP,** profondal proximal tooth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

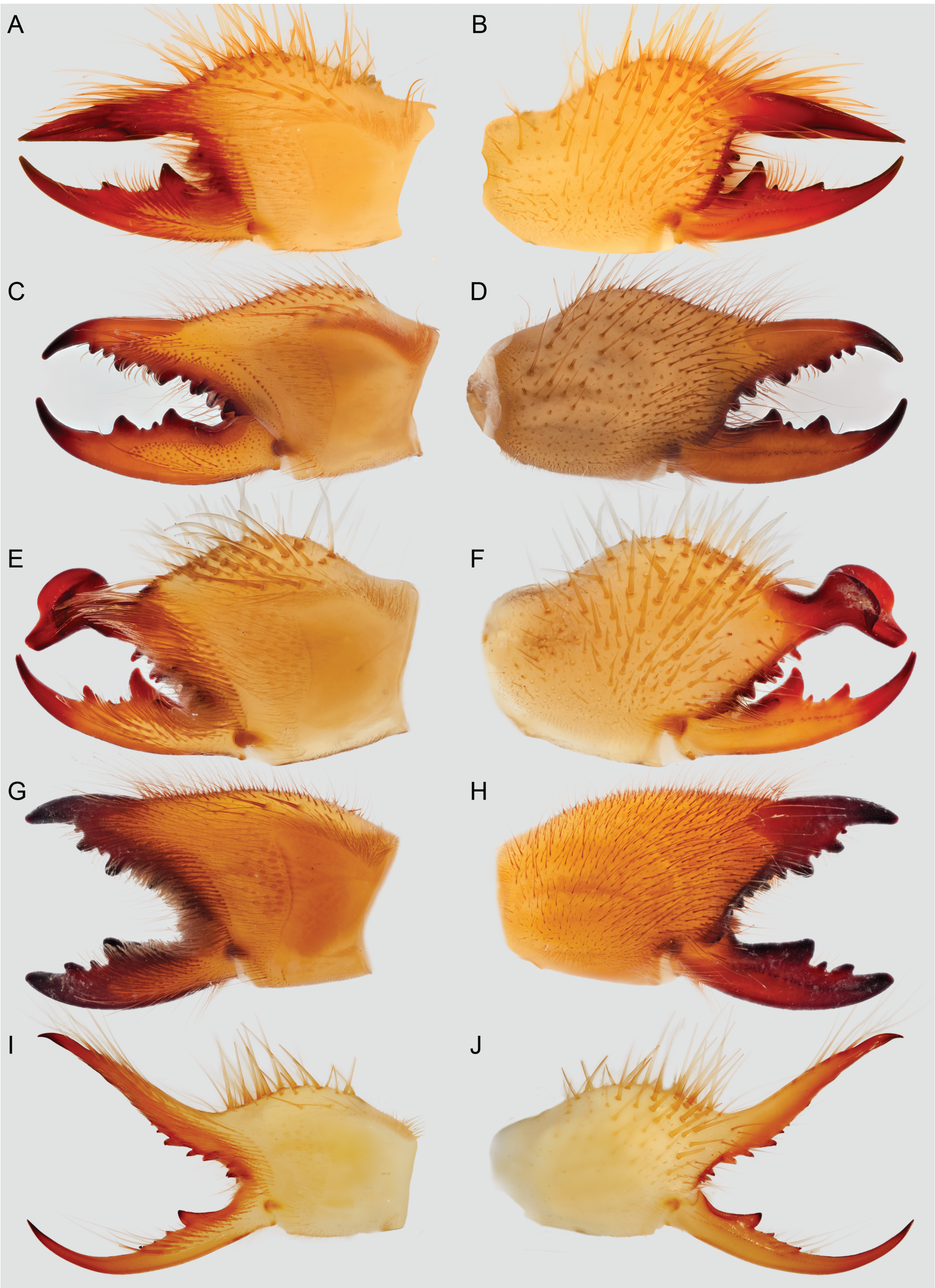


PLATE 72. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]). **C, D.** *Eremocosta gigasella* (Muma, 1970), ♀ (DMNS ZA.17350). **E, F.** *Eremothera sculpturata* Muma, 1951, ♂ (DMNS ZA.16475). **G, H.** *Eremorhax joshui* (Brookhart and Muma, 1987), ♀ (DMNS ZA.16415). **I, J.** *Chanbria regalis* Muma, 1951, ♂ (AMNH [LP 10746]).

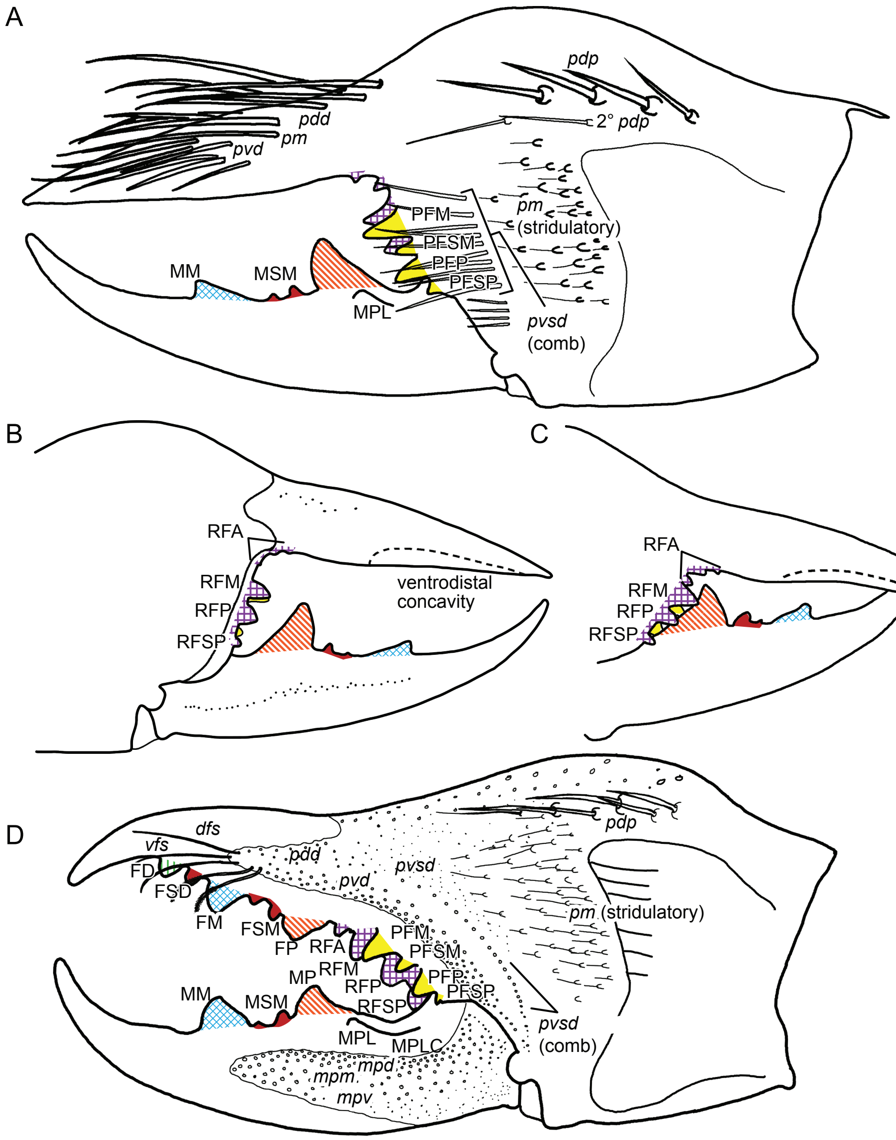

A
pdp
pdd
pm
pvd
2° pdp
PFM
PFSM
PFP
PFSP
pm
(stridulatory)
MM
MSM
MPL
pvsd
(comb)
B
RFA
RFM
RFP
RFSP
ventrodistal
concavity
C
RFA
RFM
RFP
RFSP
D
dfs
vfs
FD
FSD
FM
FSM
FP
RFA
pdd
pvd
pvsd
pdp
pm (stridulatory)
PFM
PFSM
PFP
PFSP
MP
RFM
RFP
RFSP
MM
MSM
MPL
MPLC
mpd
mpm
mpv
pvsd
(comb)

PLATE 73. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, D**) and retrolateral (**B, C**) views, illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). **A–C.** *Eremocosta titania* (Muma, 1951). **A, B.** ♂ (AMNH [LP 5035]). **C.** ♂ (MNHN). **D.** *Eremocosta gigasella* (Muma, 1970), ♀ (DMNS ZA.17350). Abbreviations: ***dfs*,** dorsal flagellar seta; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***mpd*,** movable finger, prodorsal setae; **MPL,** movable finger, prolateral tooth; **MPLC,** movable finger, prolateral carina; ***mpm*,** movable finger, promedial setae; ***mpv*,** movable finger, proventral setae; **MSM,** movable finger, submedial teeth; ***pdd*,** prodorsal distal setae; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pm*,** promedial setae (including stridulatory setae); ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae (including setal comb); **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth; ***vfs*,** ventral flagellar seta; **2°,** secondary.

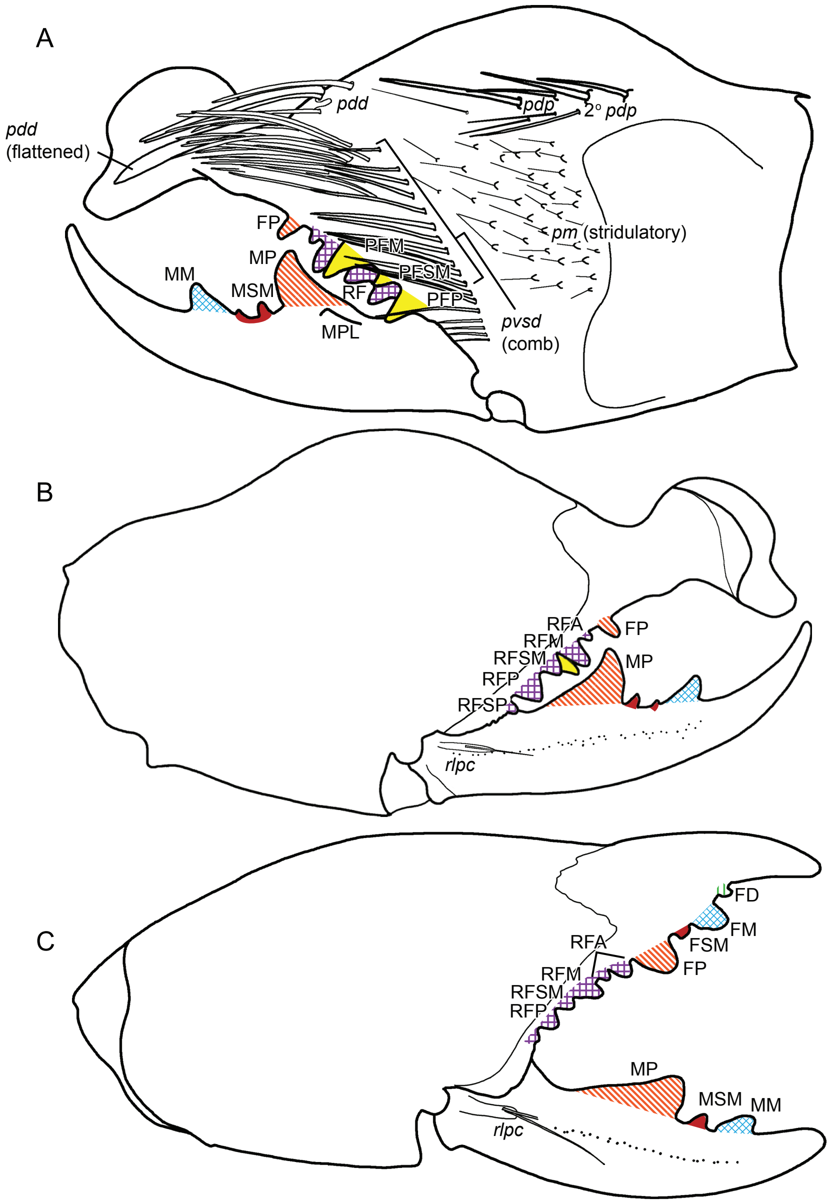

A
pdd
pdp
2° pdp
pdd
(flattened)
FP
PFM
pm (stridulatory)
MP
PFSM
MM
MSM
RF
PFP
pvsd
(comb)
MPL
B
RFA
FP
RFM
RFSM
MP
RFP
RFSP
rlpc
C
FD
FM
RFA
FSM
FP
RFM
RFSM
RFP
MP
MSM
MM
rlpc

PLATE 74. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). **A, B.** *Eremothera sculpturata* Muma, 1951, ♂ (DMNS ZA.16475). **C.** *Eremorhax joshui* (Brookhart and Muma, 1987), ♀ (DMNS ZA.16415). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MSM,** movable finger, submedial teeth; ***pdd*,** prodorsal distal setae; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; ***pm*,** promedial setae (stridulatory setae only); ***pvsd*,** proventral subdistal setae (including setal comb); **RF,** retrofondal teeth; **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster; **2°,** secondary.

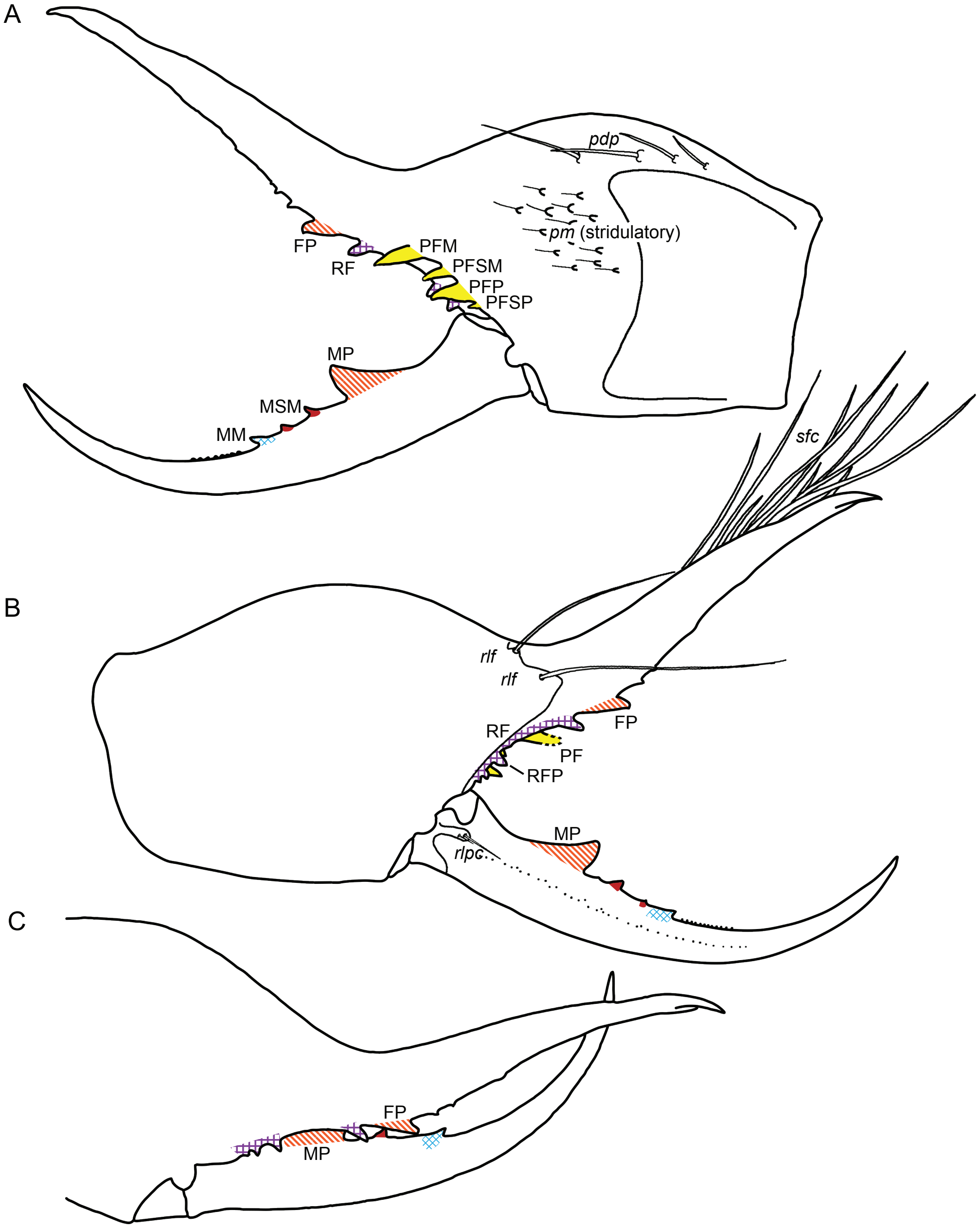


PLATE 75. Eremobatidae Kraepelin, 1899, *Chanbria regalis* Muma, 1951, ♂ (AMNH [LP 10746]), chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). Abbreviations: **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; ***pdp*,** prodorsal proximal setae; **PF,** profondal teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pm*,** promedial setae (stridulatory setae only); **RF,** retrofondal teeth; **RFP,** retrofondal proximal tooth; ***rlf*,** retrolateral finger setae; ***rlpc*,** retrolateral proximal setal cluster; ***sfc*,** setiform flagellar complex.

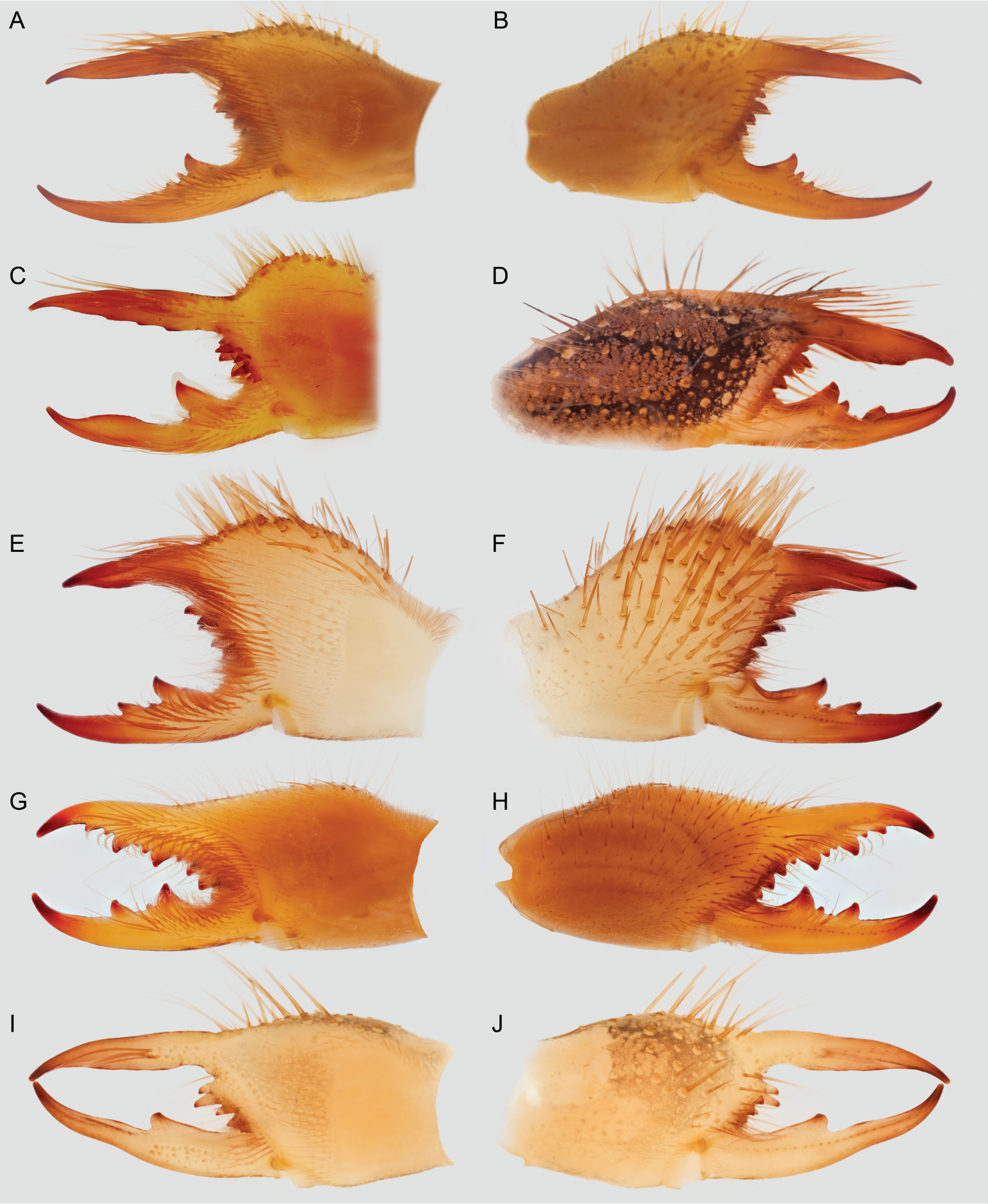


PLATE 76. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Eremochelis acrilobatus* (Muma, 1962), ♂ (DMNS ZA.16067). **C.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH). **D.** *Eremochelis albaventralis* Brookhart and Cushing, 2005, paratype ♂ (DMNS ZA.17382). **E–H.** *Eremochelis insignatus* Roewer, 1934. **E, F.** ♂ (DMNS ZA.25434). **G, H.** ♀ (DMNS ZA.16136). **I, J.** *Eremochelis oregonensis* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10008).

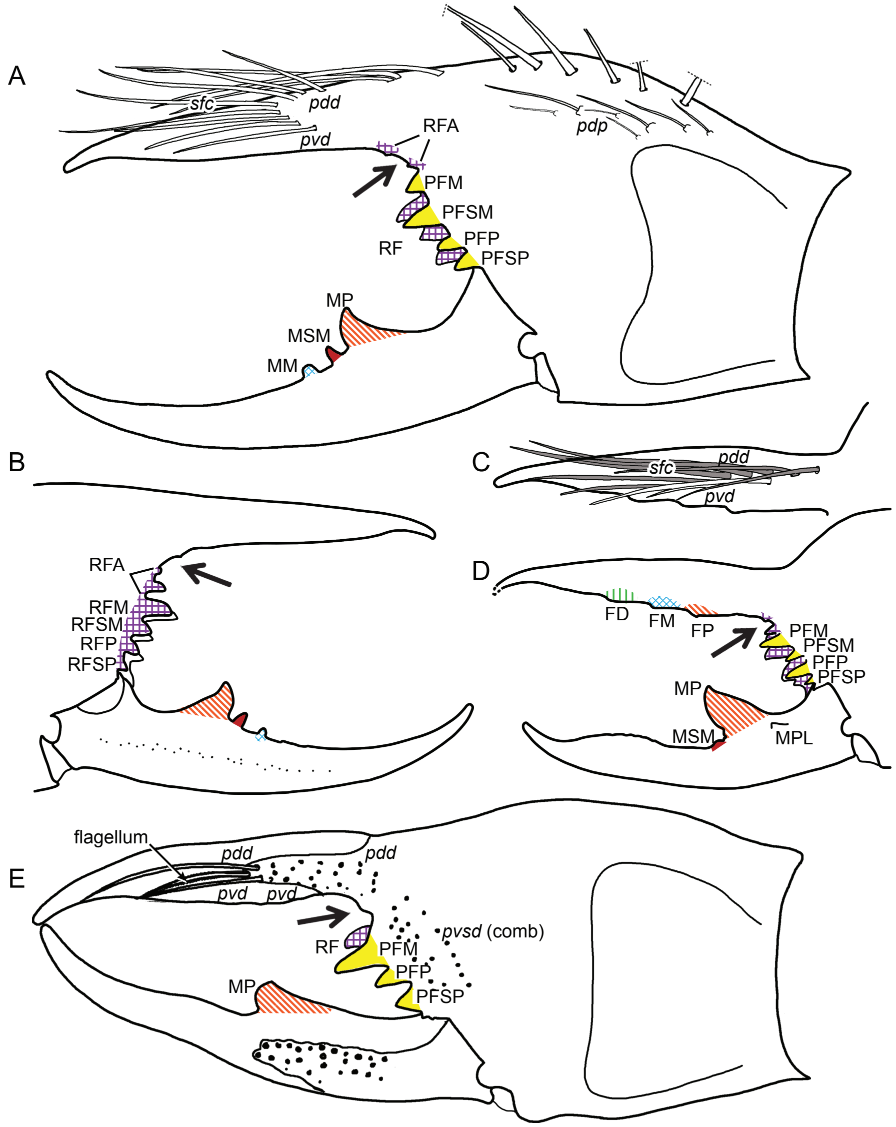

A
sfc
pdd
pvd
RFA
pdp
PFM
PFSM
RF
PFP
PFSP
MP
MSM
MM
B
RFA
RFM
RFSM
RFP
RFSP
C
sfc
pdd
pvd
D
FD
FM
FP
PFM
PFSM
PFP
PFSP
MP
MSM
MPL
flagellum
pdd
pdd
E
pvd
pvd
pvsd (comb)
RF
PFM
PFP
MP
PFSP

PLATE 77. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, D, E**) and retrolateral (**B**) views, and fixed (dorsal) finger, prolateral view (**C**), illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). **A.** *Eremochelis acrilobatus* (Muma, 1962), ♂ (DMNS ZA.16067). **B–D.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH), with closeup of dorsal finger illustrating arrangement of apical setae (**B**). **E.** *Eremochelis oregonensis* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10008). Arrows indicate weakly developed fondal notch. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MSM,** movable finger, submedial tooth; ***pdd*,** prodorsal distal setae; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae (including setal comb); **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth (denticles); **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***sfc*,** setal flagellar complex.

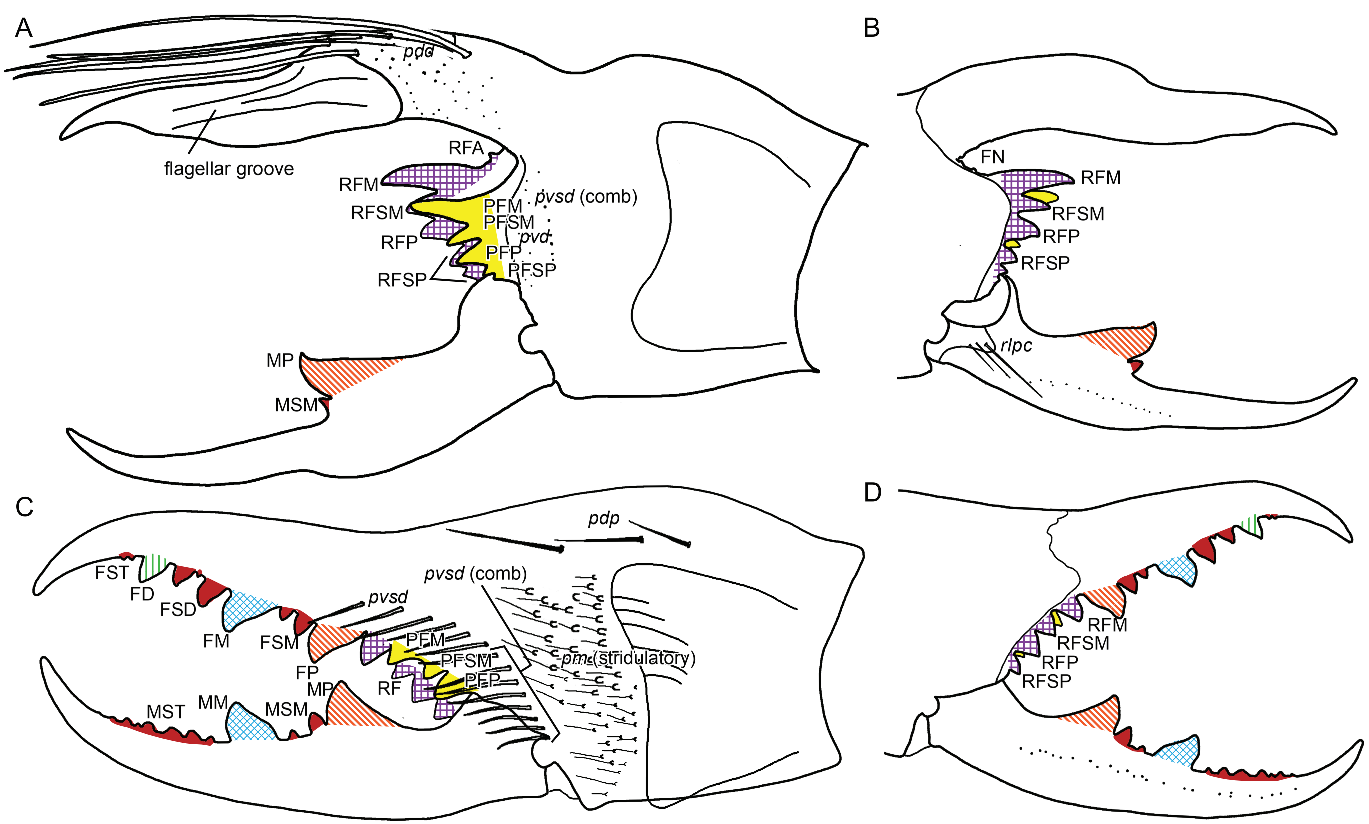

A
pdd
flagellar groove
RFA
RFM
RFSM
RFP
RFSP
PFM
PFSM
pvsd (comb)
pvd
PFP
PFSP
MP
MSM
B
FN
RFM
RFSM
RFP
RFSP
rlpc
C
pdp
pvsd (comb)
pvsd
FST
FD
FSD
FM
FSM
FP
MP
PFM
PFSM
PFP
RF
pm (stridulatory)
MST
MM
MSM
D
RFM
RFSM
RFP
RFSP

PLATE 78. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). **A, B.** *Eremochelis bilobatus* (Muma, 1951), ♂ (DMNS ZA.16039). **C, D.** *Horribates bantai* Muma, 1989, ♀ (DMNS ZA.17691). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FN,** fondal notch; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **FST,** fixed finger, subterminal tooth (denticle); **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **MST,** movable finger, subterminal teeth; ***pdd,*** prodorsal distal setae; ***pdp,*** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pm,*** promedial setae (stridulatory setae only); ***pvd,*** proventral distal setae; ***pvsd,*** proventral subdistal setae (including setal comb); **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth (denticles); **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc,*** retrolateral proximal setal cluster.

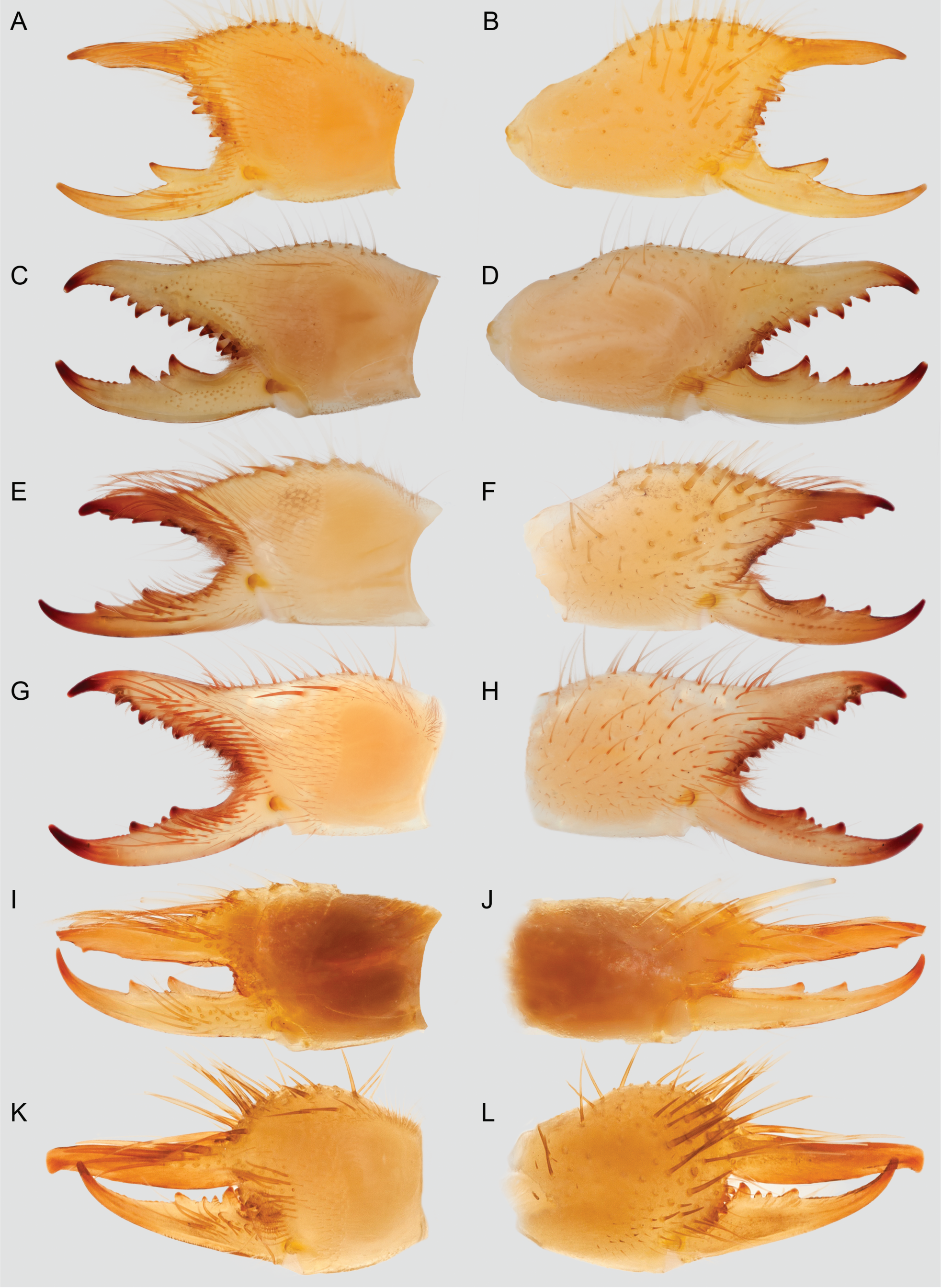


PLATE 79. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I, K**) and retrolateral (**B, D, F, H, J, L**) views. **A–D.** *Hemerotrecha fruitana* Muma, 1951. **A, B.** ♂ (DMNS ZA.17312). **C, D.** ♀ (DMNS ZA.17313). **E–H.** *Hemerotrecha branchi* Muma, 1951. **E, F.** ♂ (DMNS ZA.16786). **G, H.** ♀ (DMNS ZA.16786). **I, J.** *Hemerotrecha cornuta* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10005). **K, L.** *Hemerotrecha prenticei* Brookhart and Cushing, 2008, holotype ♂ (DMNS ZA.21376).

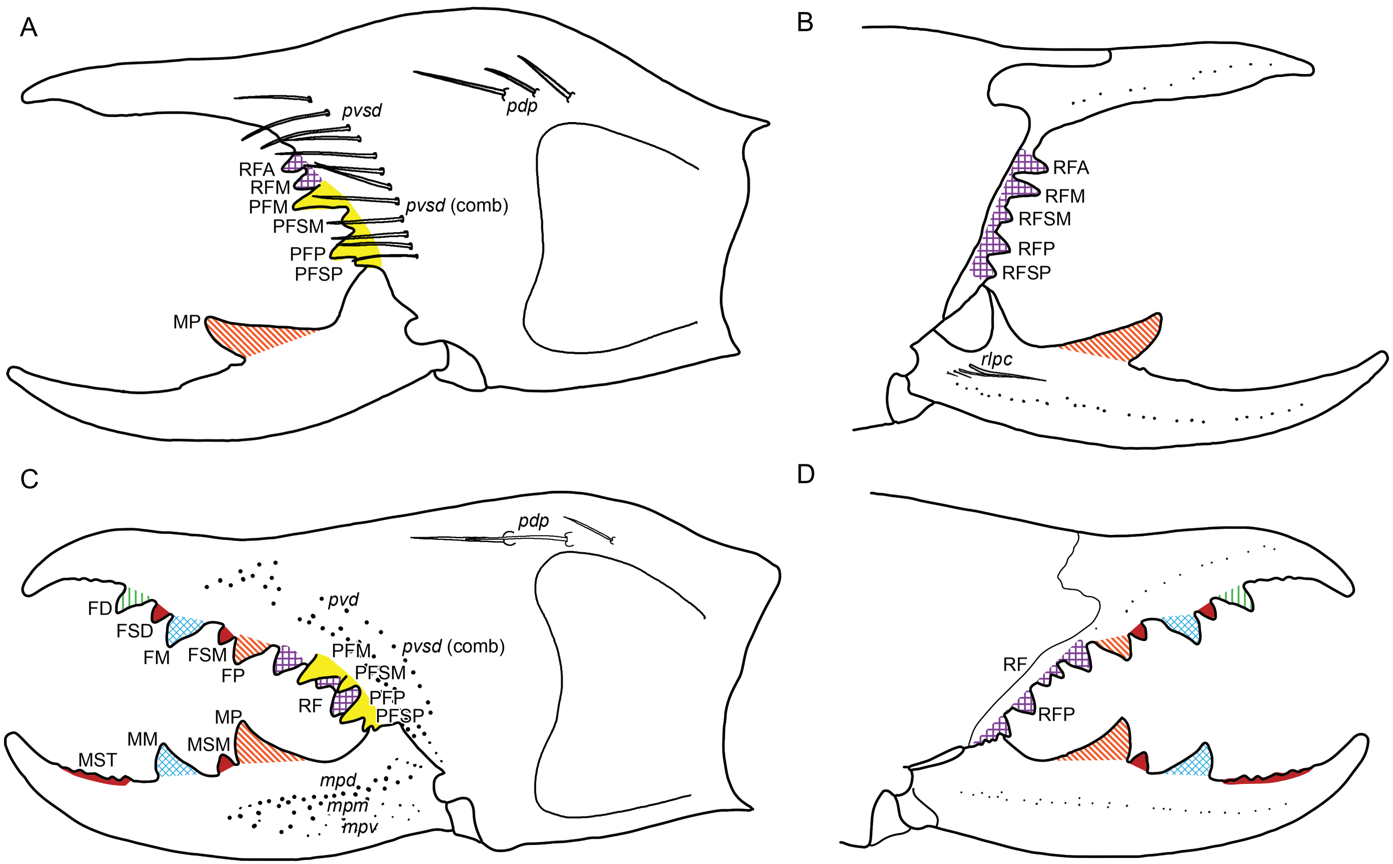

A
pvsd
pdp
RFA
RFM
PFM
pvsd (comb)
PFSM
PFP
PFSP
MP
B
RFA
RFM
RFSM
RFP
RFSP
rlpc
C
pdp
pvd
FD
FSD
FM
FSM
FP
PFM
pvsd (comb)
PFSM
PFP
RF
PFSP
MP
MM
MSM
MST
mpd
mpm
mpv
D
RF
RFP

PLATE 80. Eremobatidae Kraepelin, 1899, *Hemerotrecha fruitana* Muma, 1951, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). **A, B.** ♂ (DMNS ZA.17312). **C, D.** ♀ (DMNS ZA.17313). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***mpd*,** movable finger, prodorsal setae; ***mpm*,** movable finger, promedial setae; ***mpv*,** movable finger, proventral setae; **MSM,** movable finger, submedial tooth; **MST,** movable finger, subterminal teeth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae (including setal comb); **RF,** retrofondal teeth; **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

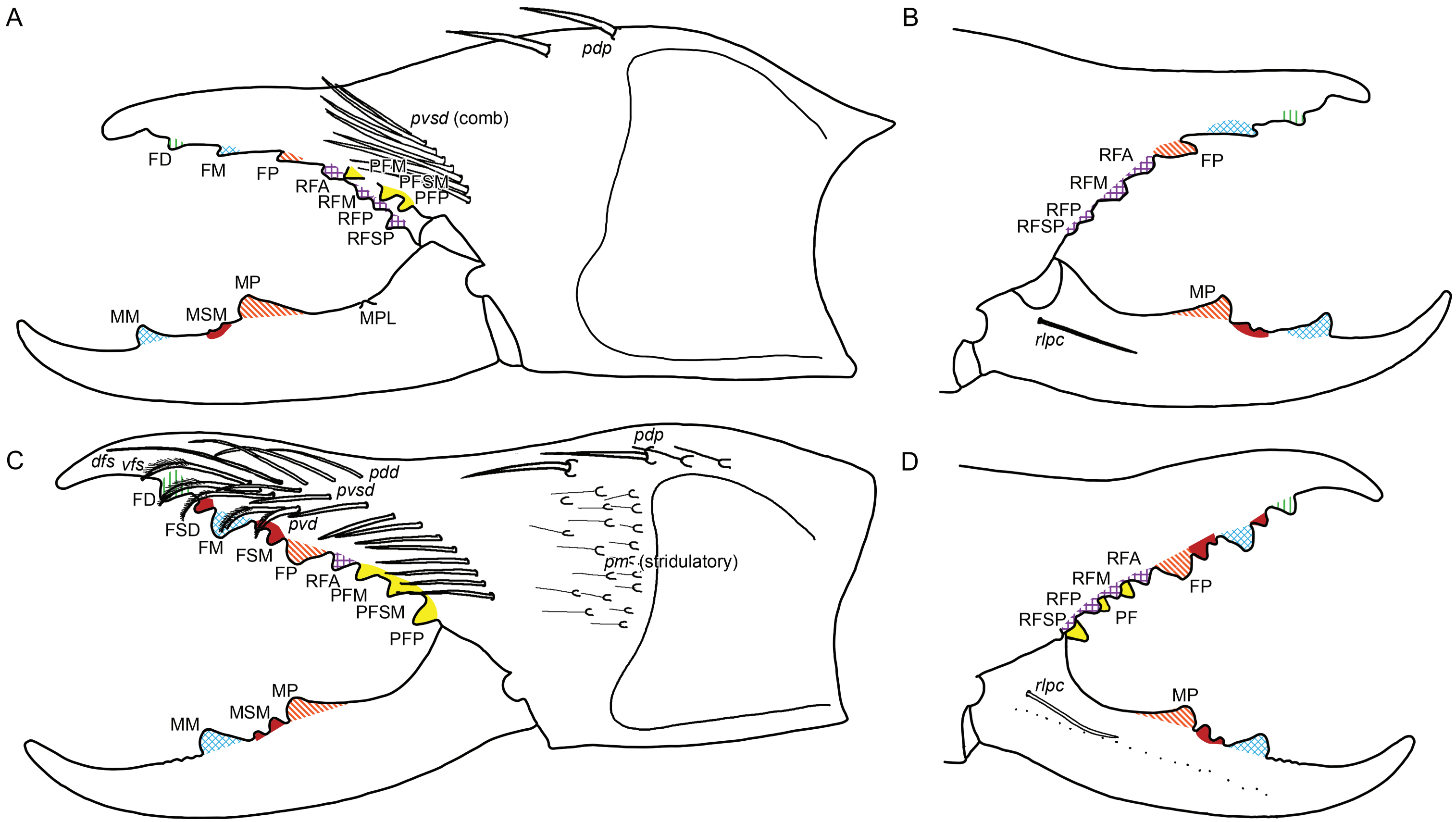

A
pdp
pvsd (comb)
FD
FM
FP
PFM
PFSM
PFP
RFA
RFM
RFP
RFSP
MP
MM
MSM
MPL
B
RFA
FP
RFM
RFP
RFSP
MP
rlpc
C
pdp
dfs
vfs
pdd
pvsd
FD
FSD
pvd
FM
FSM
FP
RFA
PFM
PFSM
PFP
pm (stridulatory)
MP
MSM
MM
D
RFA
RFM
FP
RFP
RFSP
PF
rlpc
MP

PLATE 81. Eremobatidae Kraepelin, 1899, *Hemerotrecha branchi* Muma, 1951, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and type A setiform flagellar complex (*type A sfc*). **A, B.** ♂ (DMNS ZA.16786). **C, D.** ♀ (DMNS ZA.16786). Abbreviations: ***dfs,*** dorsal flagellar seta; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MSM,** movable finger, submedial teeth; ***pdd,*** prodorsal distal setae; ***pdp,*** prodorsal proximal setae; **PF,** profondal teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; ***pm,*** promedial setae (stridulatory setae only); ***pvd,*** proventral distal setae; ***pvsd,*** proventral subdistal setae (including setal comb); **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc,*** retrolateral proximal setal cluster; ***vfs,*** ventral flagellar seta.

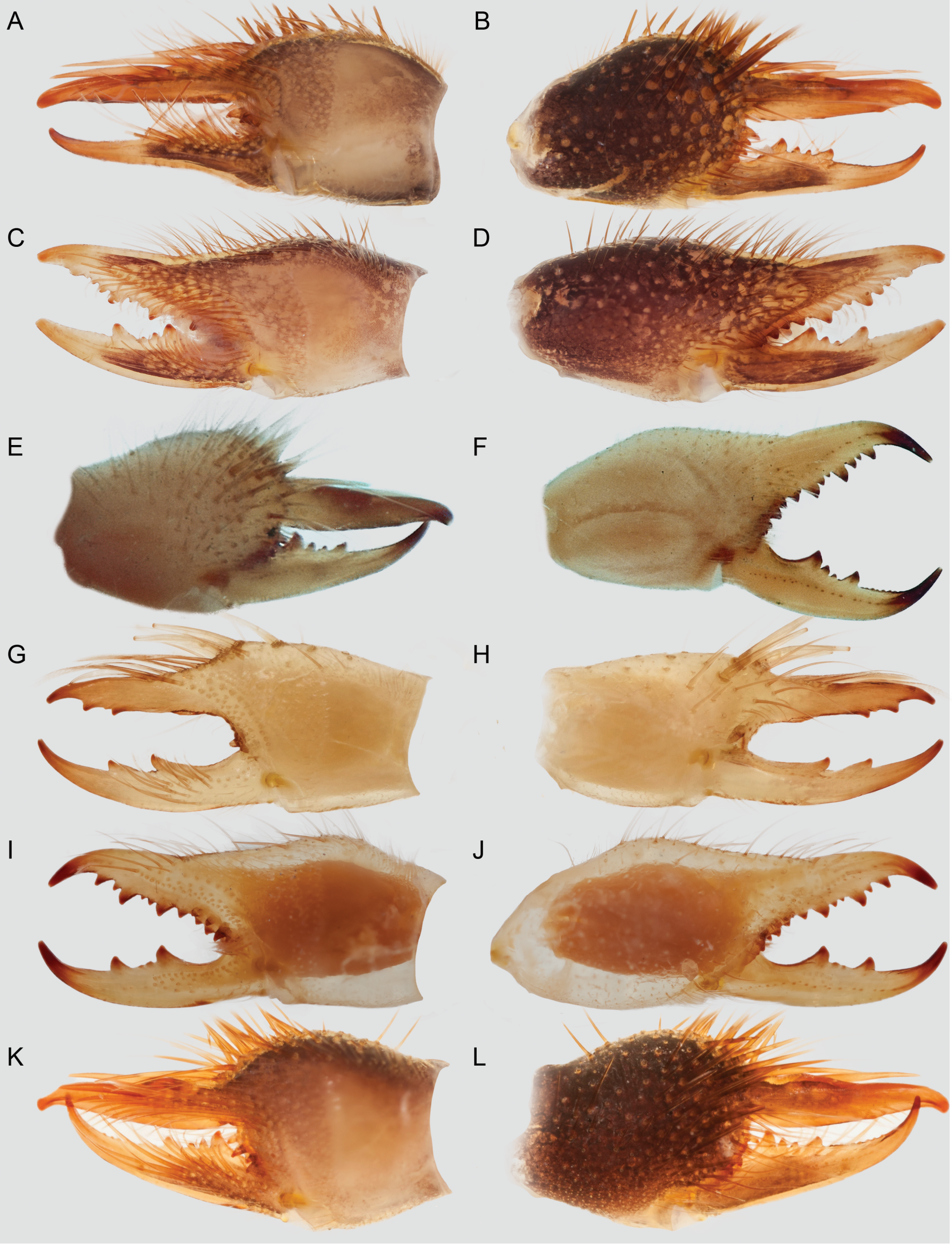


PLATE 82. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I, K**) and retrolateral (**B, D, F, H, J, L**) views. **A–D.** *Hemerotrecha hanfordana* Brookhart and Cushing, 2008. **A, B.** Holotype ♂ (DMNS ZA.21371). **C, D.** Paratype ♀ (DMNS ZA.19402). **E, F.** *Hemerotrecha marginata* (Kraepelin, 1911). **E.** Syntype ♂ (ZMUH). **F.** Syntype ♀ (ZMUH). **G–J** *Hemerotrecha sevilleta* Brookhart and Cushing, 2002. **G, H.** Holotype ♂ (DMNS ZA.10006). **I, J.** Paratype ♀ (DMNS ZA.10007). **K, L.** *Hemerotrecha vetteri* Brookhart and Cushing, 2008, holotype ♂ (DMNS ZA.21377).

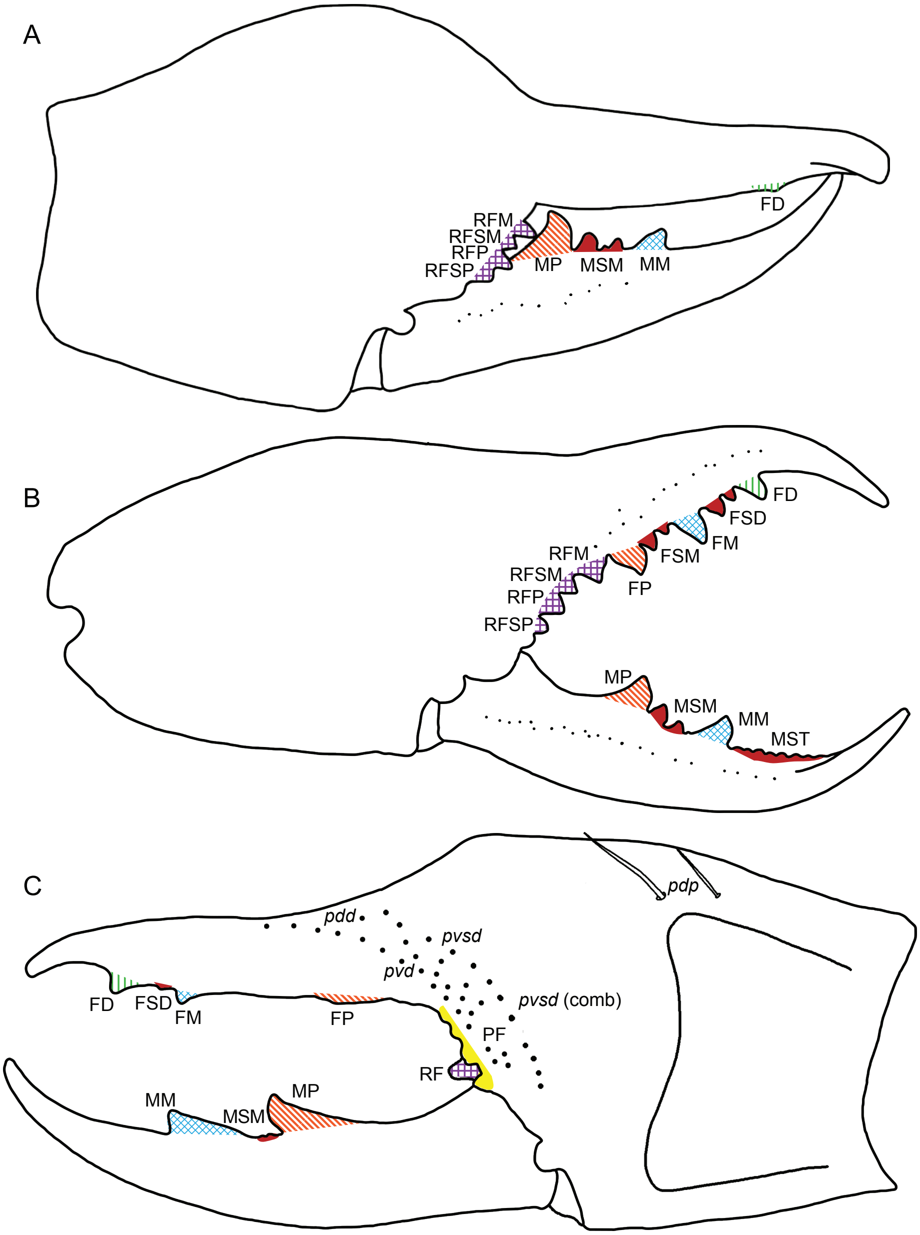

A
RFM
RFSM
RFP
RFSP
MP
MSM
MM
FD
B
FD
FSD
FM
FSM
RFM
RFSM
RFP
RFSP
FP
MP
MSM
MM
MST
C
pdp
pdd
pvsd
pvd
pvsd (comb)
FD
FSD
FM
FP
PF
RF
MM
MSM
MP

PLATE 83. Eremobatidae Kraepelin, 1899, chelicerae, retrolateral (**A**, **B**) and prolateral (**C**) views, illustrating dentition and setae. **A**, **B.** *Hemerotrecha marginata* (Kraepelin, 1911). **A.** Syntype ♂ (ZMUH). **B.** Syntype ♀ (ZMUH). **C.** *Hemerotrecha sevilleta* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10006). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **MST,** movable finger, subterminal teeth; ***pdd*,** prodorsal distal setae; ***pdp*,** prodorsal proximal setae; **PF,** profondal teeth; ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae (including setal comb); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

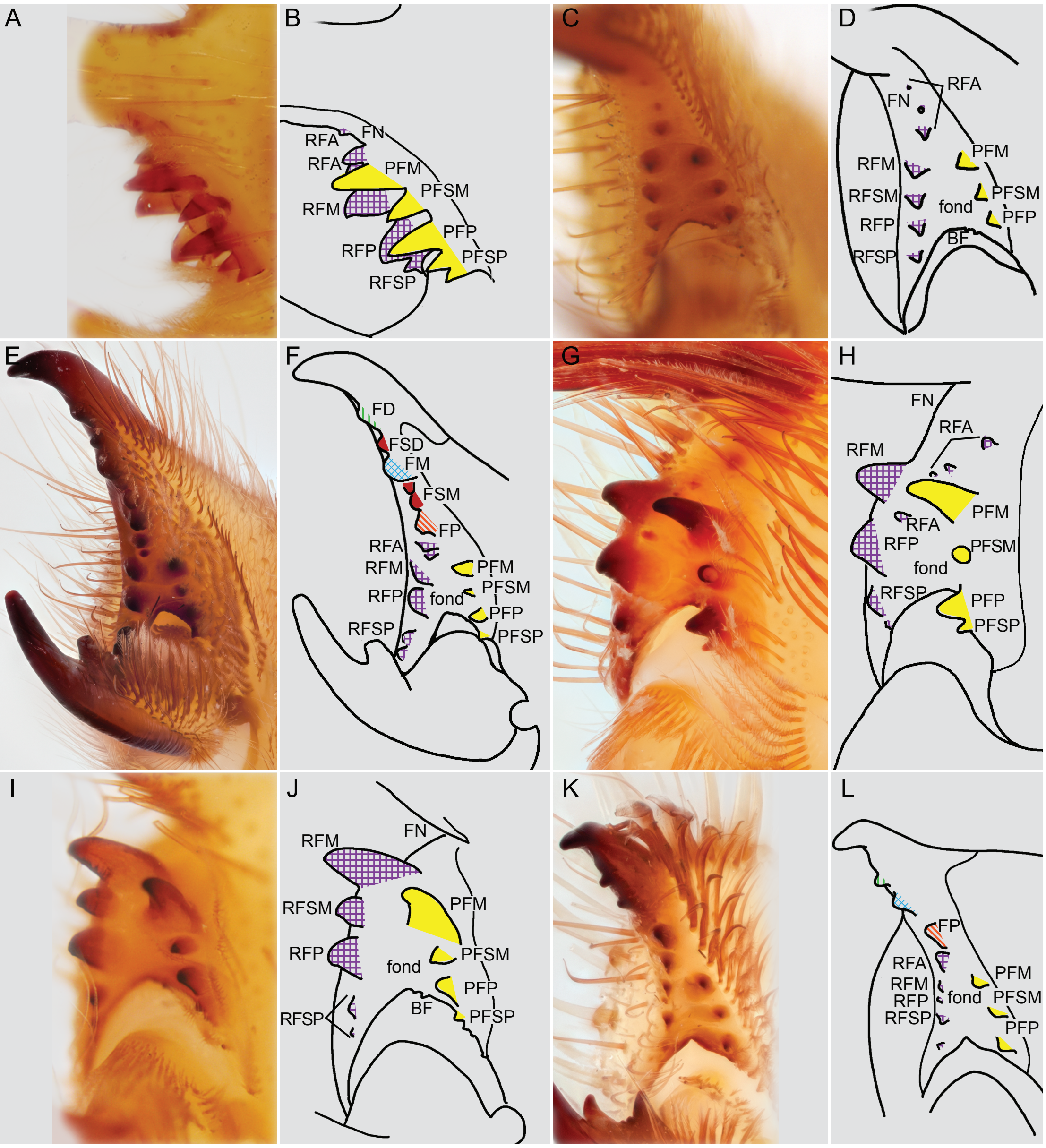

A
B
RFA
FN
RFA
PFM
PFSM
RFM
PFP
RFP
PFSP
RFSP
C
D
RFA
FN
PFM
RFM
RFSM
fond
PFSM
RFP
PFP
BF
RFSP
E
F
FD
FSD
FM
FSM
FP
RFA
RFM
PFM
PFSM
RFP
fond
PFP
RFSP
PFSP
G
H
FN
RFA
RFM
PFM
RFA
RFP
PFSM
fond
RFSP
PFP
PFSP
I
J
FN
RFM
PFM
RFSM
PFSM
RFP
fond
PFP
BF
RFSP
PFSP
K
L
FP
RFA
PFM
RFM
fond
PFSM
RFP
RFSP
PFP

PLATE 84. Eremobatidae Kraepelin, 1899, cheliceral fixed fingers, proventral views illustrating fondal area and basifondal teeth. **A, B.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH). **C, D.** *Eremochelis acrilobatus* (Muma, 1962), ♂ (DMNS ZA.16067). **E–H.** *Eremobates palpisetulosus* Fichter, 1941. **E, F.** ♀ (DMNS ZA.15686). **G, H.** ♂ (DMNS ZA.15683). **I, J.** *Eremochelis bilobatus* (Muma, 1951), ♂ (DMNS ZA.16039). **K, L.** *Hemerotrecha branchi* Muma, 1951, ♂ (DMNS ZA.16786). Abbreviations: **BF,** basifondal teeth; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FN,** fondal notch; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **RFA,** retrofondal apical teeth or denticles; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

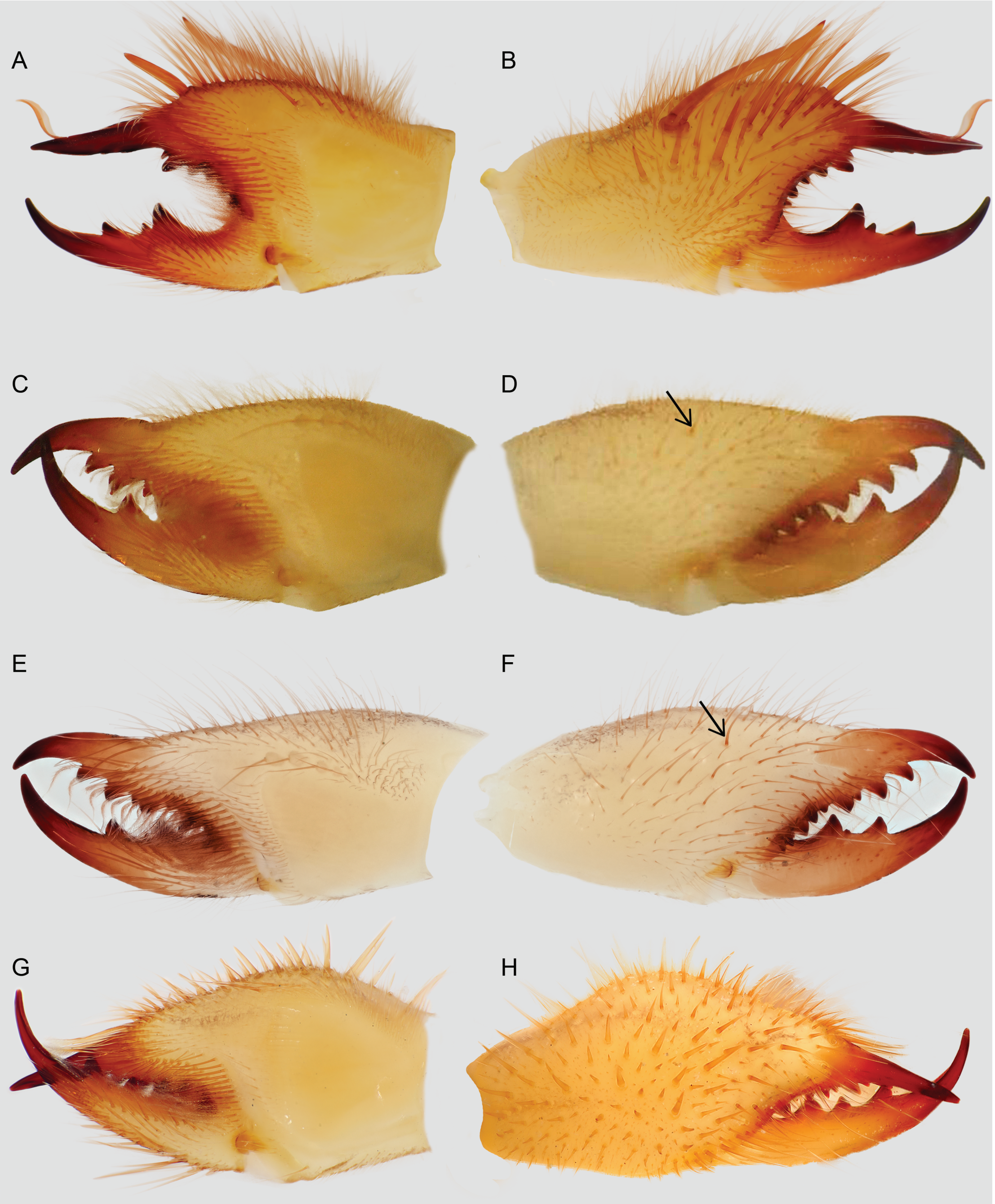


PLATE 85. Gylippinae Roewer, 1933 (**A–F**) and Lipophaginae Wharton, 1981 (**G, H**), chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A–D.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905. **A, B.** ♂ (AMNH [LP 5437]). **C, D.** ♀ (KUT) [topotype], Turkey: Kayseri Province. **E, F.** *Gylippus* (*Anoplogylippus*) *ferganensis* Birula, 1893, juv. (AMNH [LP 3921]). **G, H.** *Lipophaga trispinosa* Purcell, 1903, ♂ (NMNW 12503). Arrows indicate seta in ♀ homologous to retrolateral manus spiniform (*rlms*) seta in ♂.

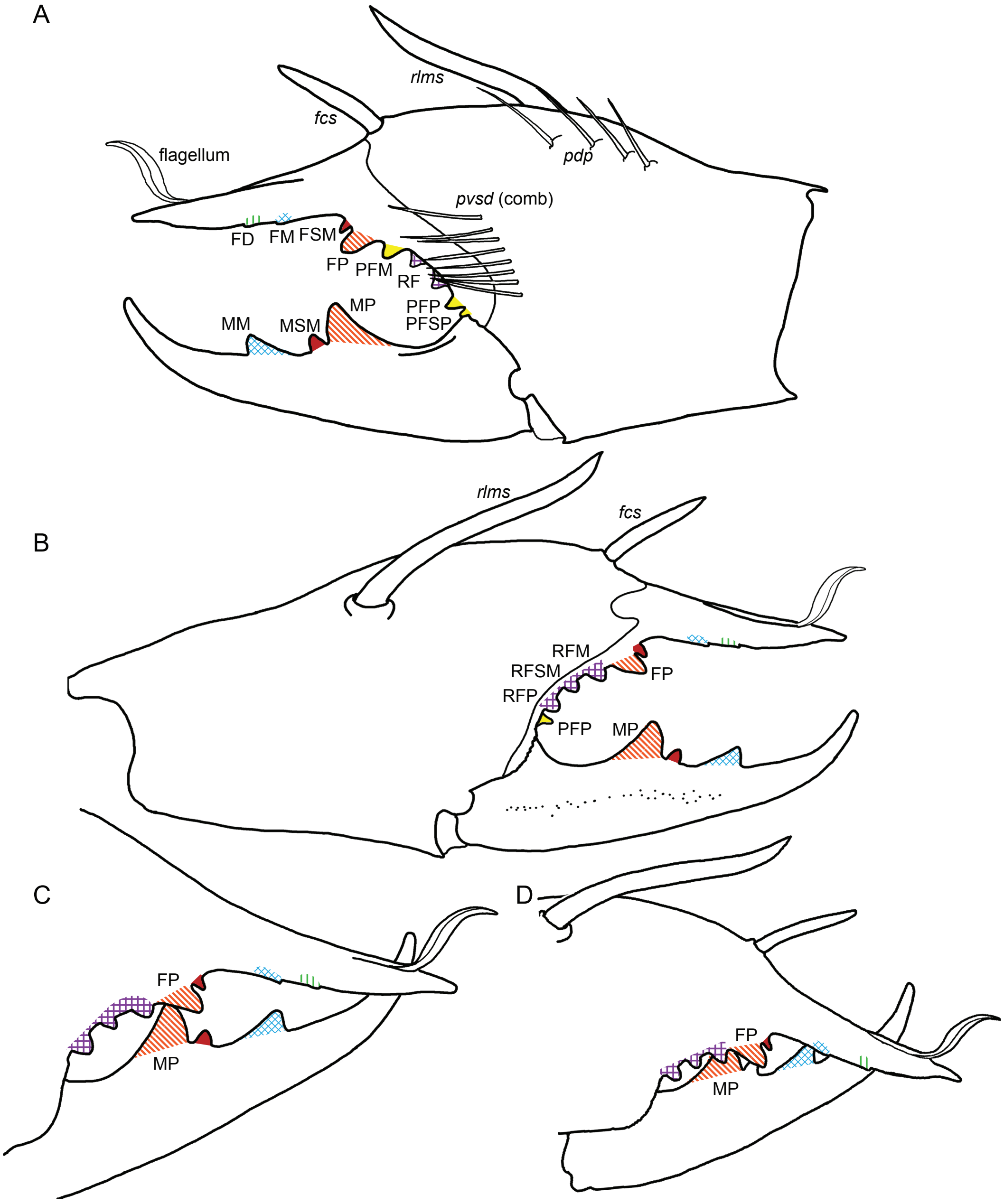

A
rlms
fcs
flagellum
pdp
pvsd (comb)
FD
FM
FSM
FP
PFM
RF
MP
PFP
PFSP
MM
MSM
B
rlms
fcs
RFM
RFSM
FP
RFP
PFP
MP
C
FP
MP
D
FP
MP

PLATE 86. Gylippinae Roewer, 1933, *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]), chelicerae, prolateral (**A**) and retrolateral (**B–D**) views, illustrating dentition, setae, and flagellar complex. Abbreviations: ***fcs*****,** flagellar complex spiniform seta; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pdp*****,** prodorsal distal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*****,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; ***rlms*****,** retrolateral manus spiniform seta.

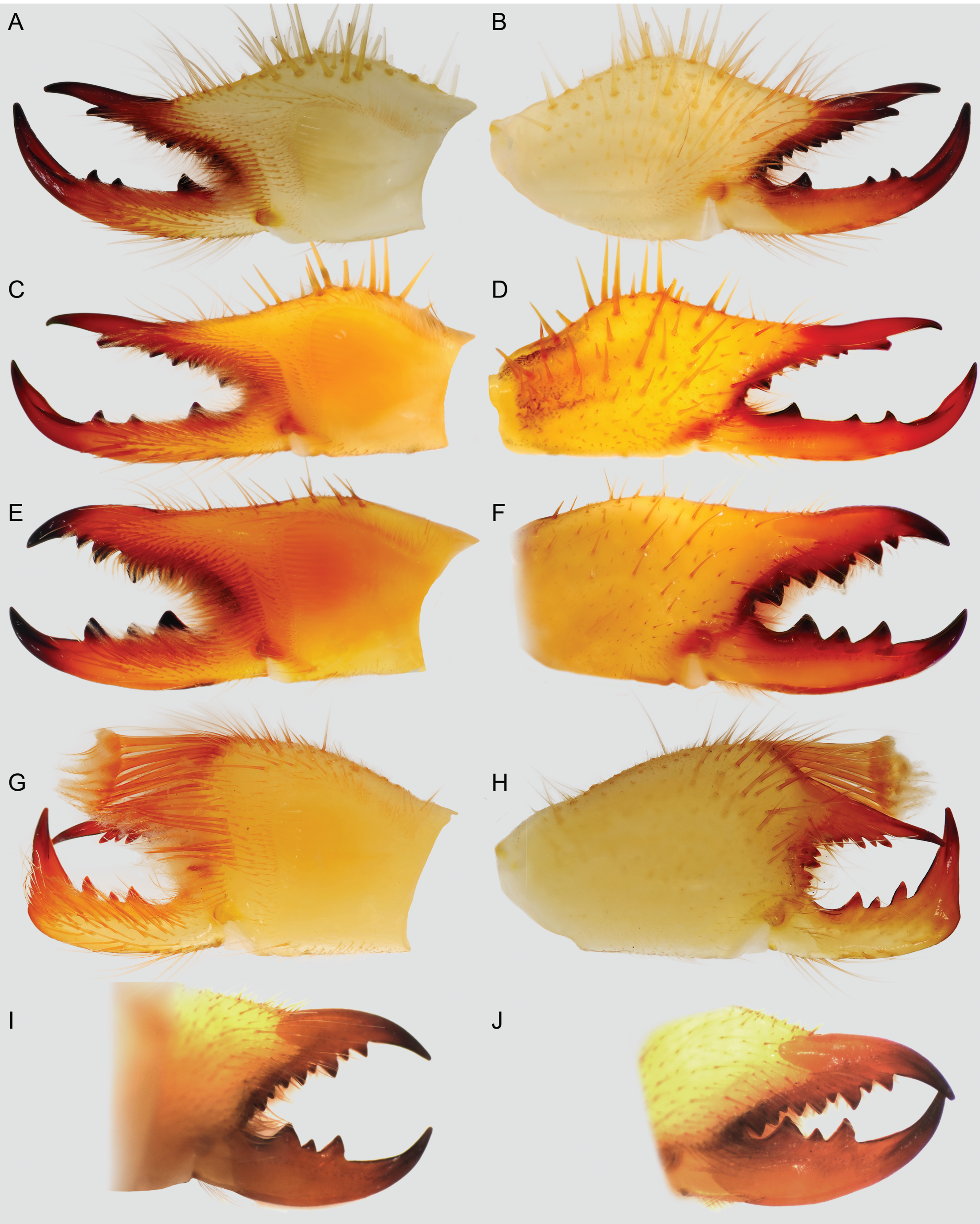


PLATE 87. Lipophaginae Wharton, 1981, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H–J**) views. **A–F.** *Trichotoma michaelseni* (Kraepelin, 1914). **A, B.** ♂ (AMNH [LP 5724]). **C, D.** ♂ (NMNW 12757). **E, F.** ♀ (NMNW 12757). **G–J.** *Bdellophaga angulata* Wharton, 1981. **G, H.** ♂ (NMNW 11601). **I, J.** ♀ (NMNW 12240), with cheliceral fingers open (**I**) and closed (**J**).

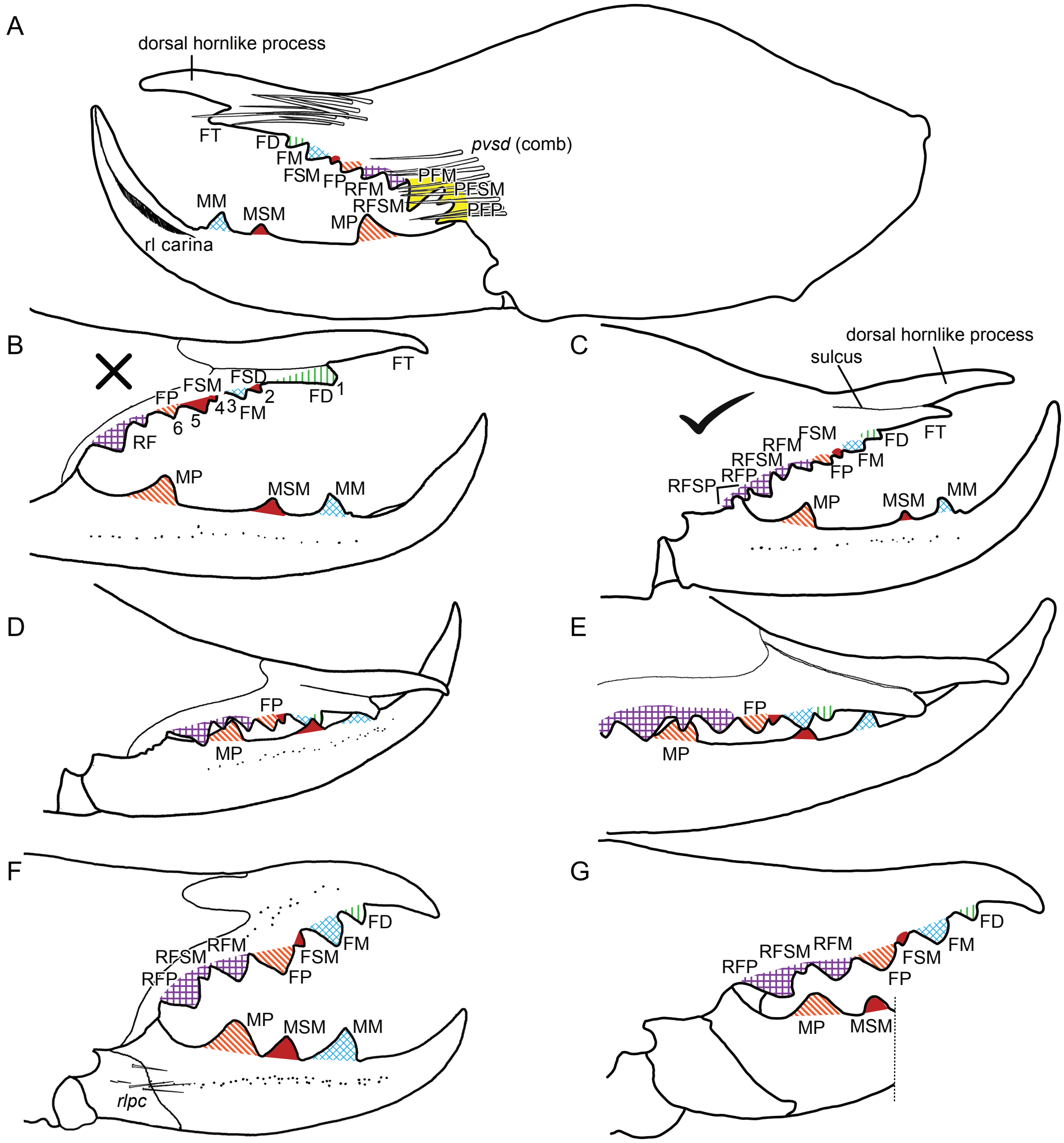

A
dorsal hornlike process
FT
FD
FM
FSM
FP
RFM
RFSM
PFM
PFSM
PFP
pvsd (comb)
MM
MSM
MP
rl carina
B
FT
FSD
FSM
FP
2
1
FD
4
3
5
6
FM
RF
MP
MSM
MM
C
dorsal hornlike process
sulcus
FSM
RFM
RFSM
RFP
RFSP
FD
FT
FM
FP
MP
MSM
MM
D
FP
MP
E
FP
MP
F
FD
FM
RFM
RFSM
RFP
FSM
FP
MP
MSM
MM
rlpc
G
FD
FM
RFM
RFSM
RFP
FSM
FP
MP
MSM

PLATE 88. Lipophaginae Wharton, 1981, *Trichotoma michaelseni* (Kraepelin, 1914), chelicerae, prolateral (**A**) and retrolateral (**B–G**) views, illustrating dentition and setae. **A, C, E.** ♂ (AMNH [LP 5724]), **B, D.** ♂ NMNW (12757), illustrating fixed (dorsal) finger interpretations of dentition by previous authors (1 = FD, 6 = FP; Roewer, 1941; Wharton, 1981), indicated by X (**B**), and proposed here (1 = FT, 2 = FD, 5 = FP), indicated by check mark (**C**). **F.** ♀ (NMNW 12757). **G.** *Trichotoma brunnea* Lawrence, 1968, ♂ (AMNH [LP 9870]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **FT,** fixed finger, terminal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; ***pvsd,*** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; **rl,** retrolateral; ***rlpc,*** retrolateral proximal setal cluster.

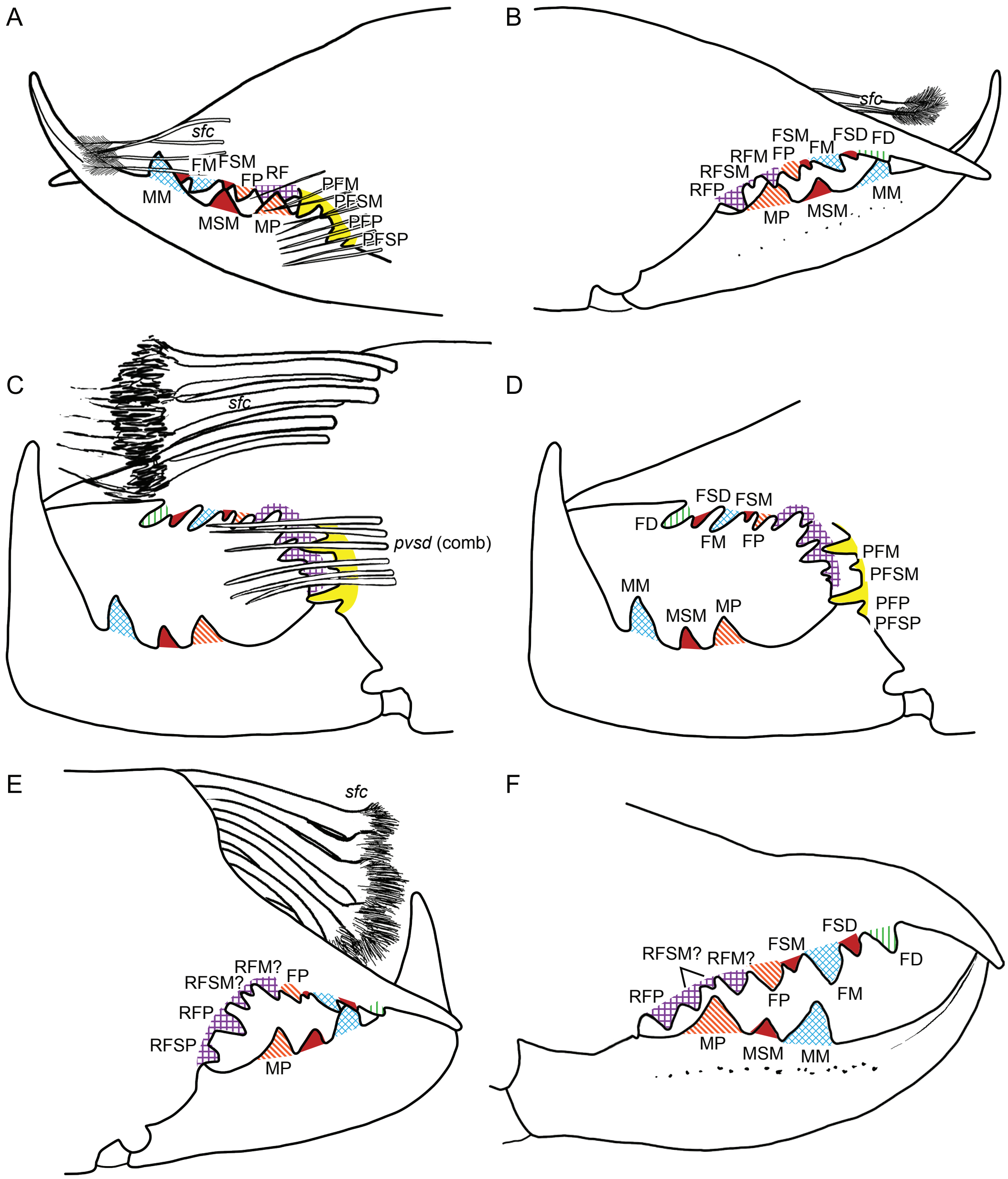

A
sfc
FM
FSM
FP
RF
MM
PFM
PFSM
MSM
MP
PFP
PFSP
B
sfc
FSM
FSD
FD
RFM
FP
FM
RFSM
RFP
MM
MP
MSM
C
sfc
pvsd (comb)
D
FSD
FSM
FD
FM
FP
PFM
PFSM
MM
MSM
MP
PFP
PFSP
E
sfc
RFM?
FP
RFSM?
RFP
RFSP
MP
F
FSD
RFSM?
RFM?
FSM
FD
RFP
FP
FM
MP
MSM
MM

PLATE 89. Lipophaginae Wharton, 1981, chelicerae, prolateral (**A, C, D**) and retrolateral (**B, E, F**) views, illustrating dentition, setae, and *type B sfc*. **A, B.** *Lipophaga trispinosa* Purcell, 1903, ♂ (NMNW 12503). **C–F.** *Bdellophaga angulata* Wharton, 1981. **C–E.** ♂ (NMNW 11601). **F.** ♀ (NMNW 12240). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***sfc*,** setiform flagellar complex.

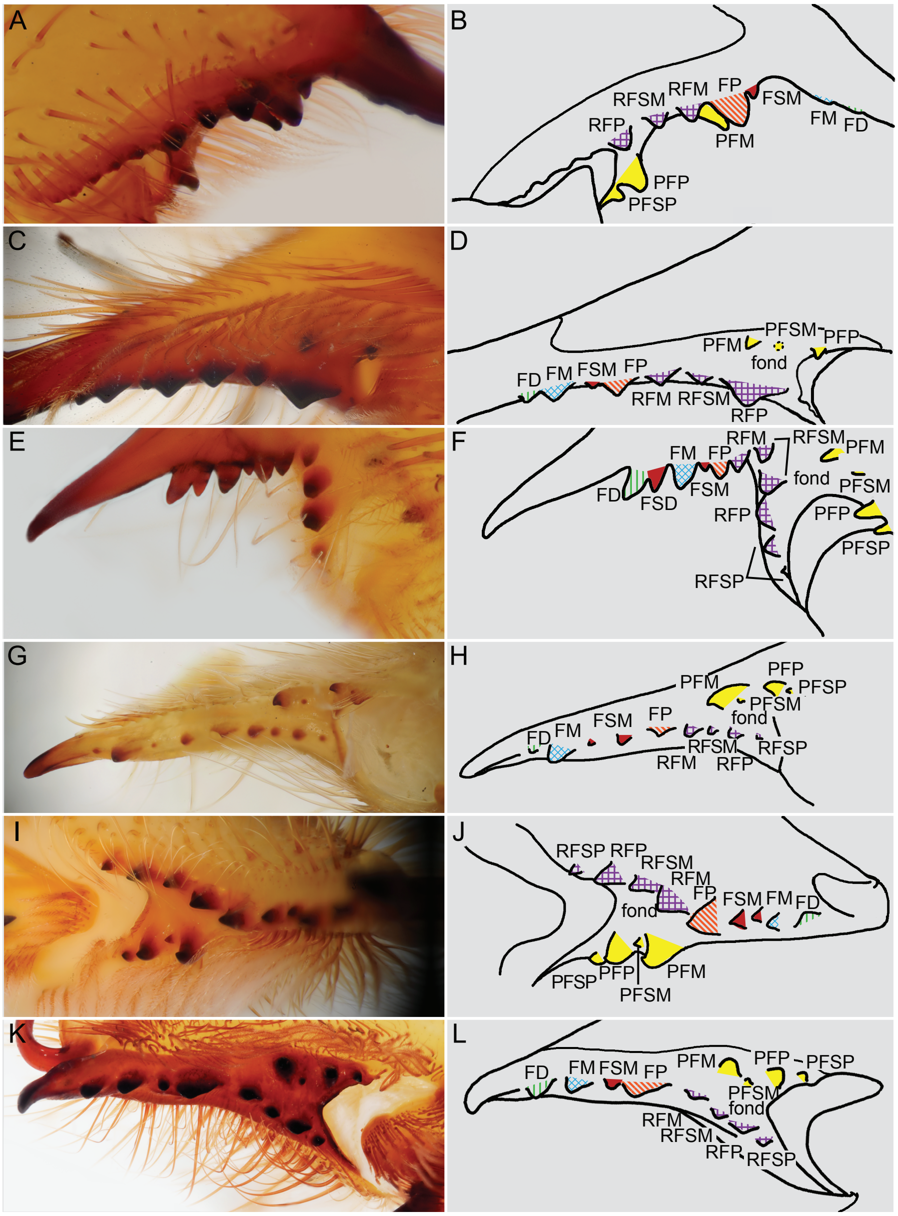

A
B
RFSM
RFM
FP
FSM
FM
FD
RFP
PFM
PFP
PFSP
C
D
PFSM
PFP
PFM
fond
FD
FM
FSM
FP
RFM
RFSM
RFP
E
F
RFM
RFSM
PFM
FM
FP
fond
PFSM
FD
FSD
FSM
RFP
PFP
PFSP
RFSP
G
H
PFP
PFM
PFSP
PFSM
FSM
FP
fond
FD
FM
RFSM
RFSP
RFM
RFP
I
J
RFSP
RFP
RFSM
RFM
FP
FSM
FM
FD
fond
PFSP
PFP
PFM
PFSM
K
L
FD
FM
FSM
FP
PFM
PFP
PFSP
PFSM
fond
RFM
RFSM
RFP
RFSP

PLATE 90. Gylippinae Roewer, 1933 (**A, B**), Lipophaginae Wharton, 1981 (**C–F**), and Solpugidae Leach, 1815 (**G–L**), cheliceral fixed fingers, retroventral (**A, B, I, J**) and proventral (**C–H, K, L**) views, illustrating fondal area. **A, B.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **C, D.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]). **E, F.** *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601). **G, H.** *Solpugisticella kenyae* Turk, 1960, holotype ♂ (HUJI). **I, J.** *Zeria sericea* (Pocock, 1897), ♂ (NMNW 13801). **K, L.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, distal tooth; **FSM,** fixed finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial teeth; **RFSP,** retrofondal subproximal teeth.

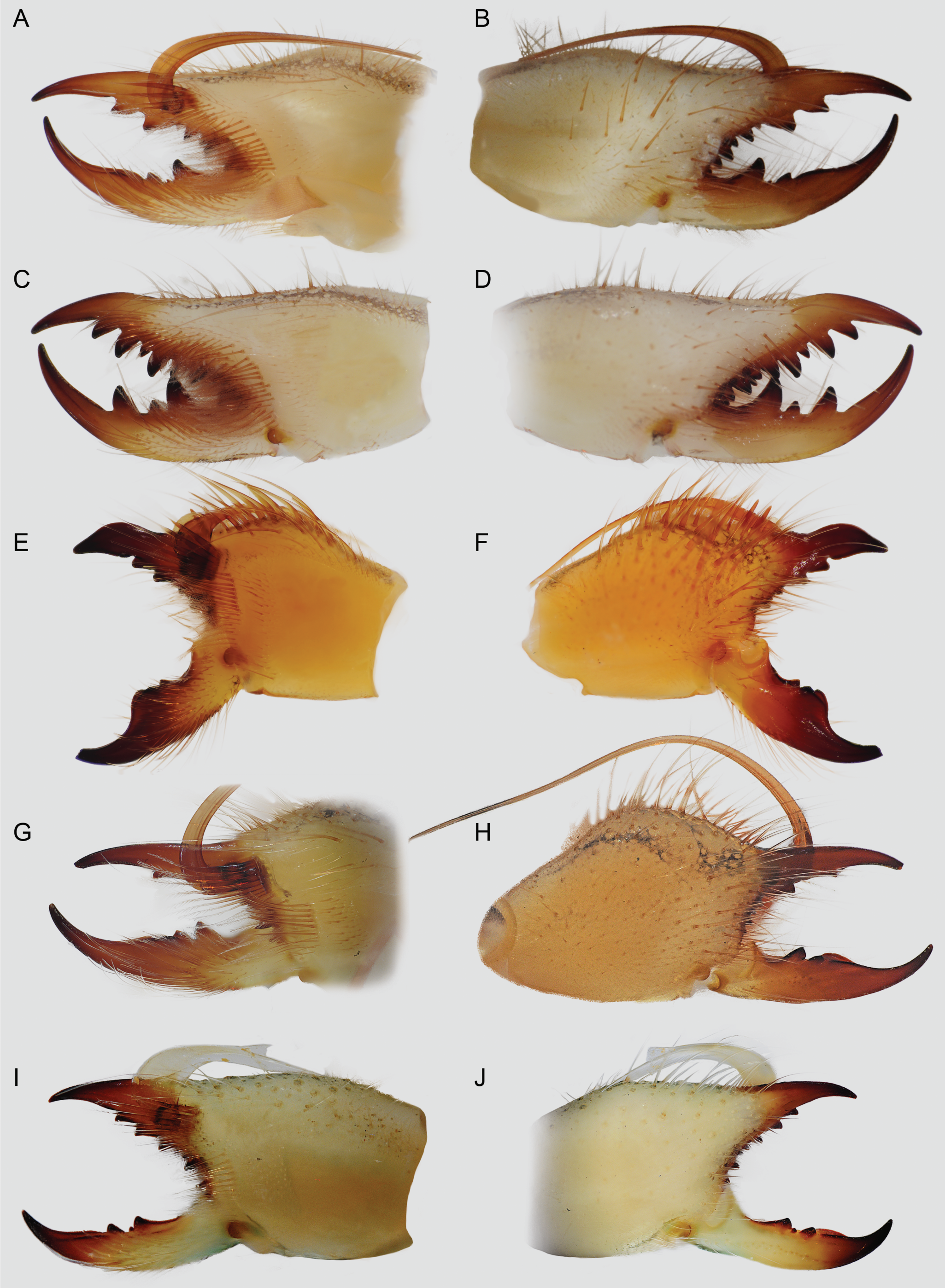


PLATE 91. Ceromidae Roewer, 1933, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Ceroma inerme* Purcell, 1899. **A, B.** ♂ (AMNH [LP 9864]). **C, D.** ♀ (AMNH [LP 8425]). **E, F.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **G, H.** *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355). **I, J.** *Ceromella* sp., ♂ (AMNH [LP 8527]).

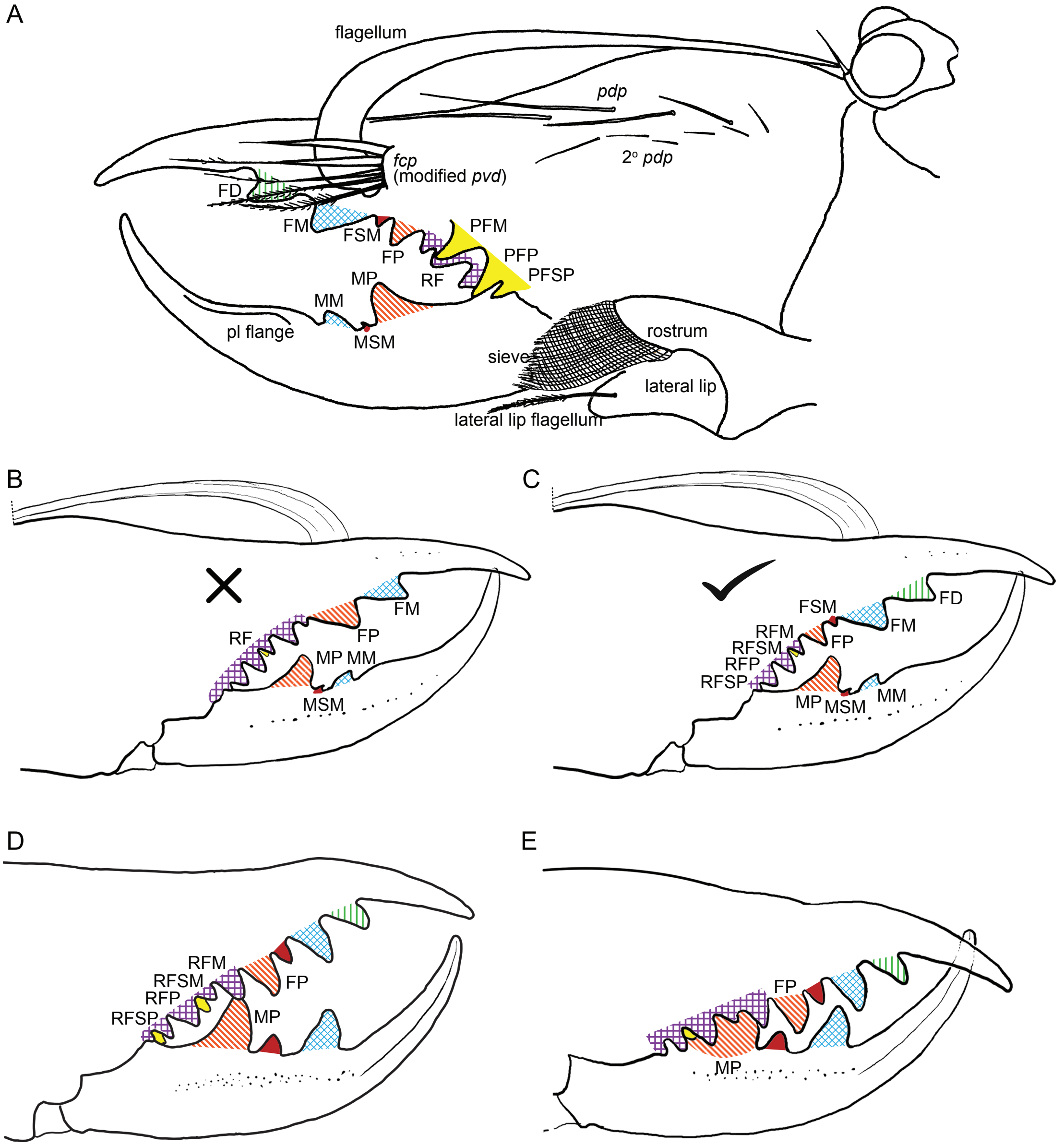

A
flagellum
pdp
fcp
(modified *pvd*)
2° *pdp*
FD
FM
FSM
PFM
FP
PFP
PFSP
MP
RF
MM
pl flange
MSM
rostrum
sieve
lateral lip
lateral lip flagellum
B
FM
RF
FP
MP MM
MSM
C
FD
FSM
FM
RFM
RFSM
FP
RFP
RFSP
MP MSM
MM
D
RFM
RFSM
FP
RFP
RFSP
MP
E
FP
MP

PLATE 92. Ceromidae Roewer, 1933, *Ceroma inerme* Purcell, 1899, chelicerae, prolateral (**A**) and retrolateral (**B–E**) views, illustrating interpretations of fixed finger dentition by previous authors (Purcell, 1899; Roewer, 1934: 323; Wharton, 1981), indicated by X (**B**), and proposed here, indicated by check mark (**C**), setae, and flagellar complex. **A–C.** ♂ (AMNH [LP 9864]). **D, E.** ♀ (AMNH [LP 8425]). Abbreviations: ***fcp*,** flagellum complex plumose setae (modified *pvd* setae); **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **pl,** prolateral; ***pvd*,** proventral distal setae; **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial teeth; **RFSP,** retrofondal subproximal teeth; **2°,** secondary.

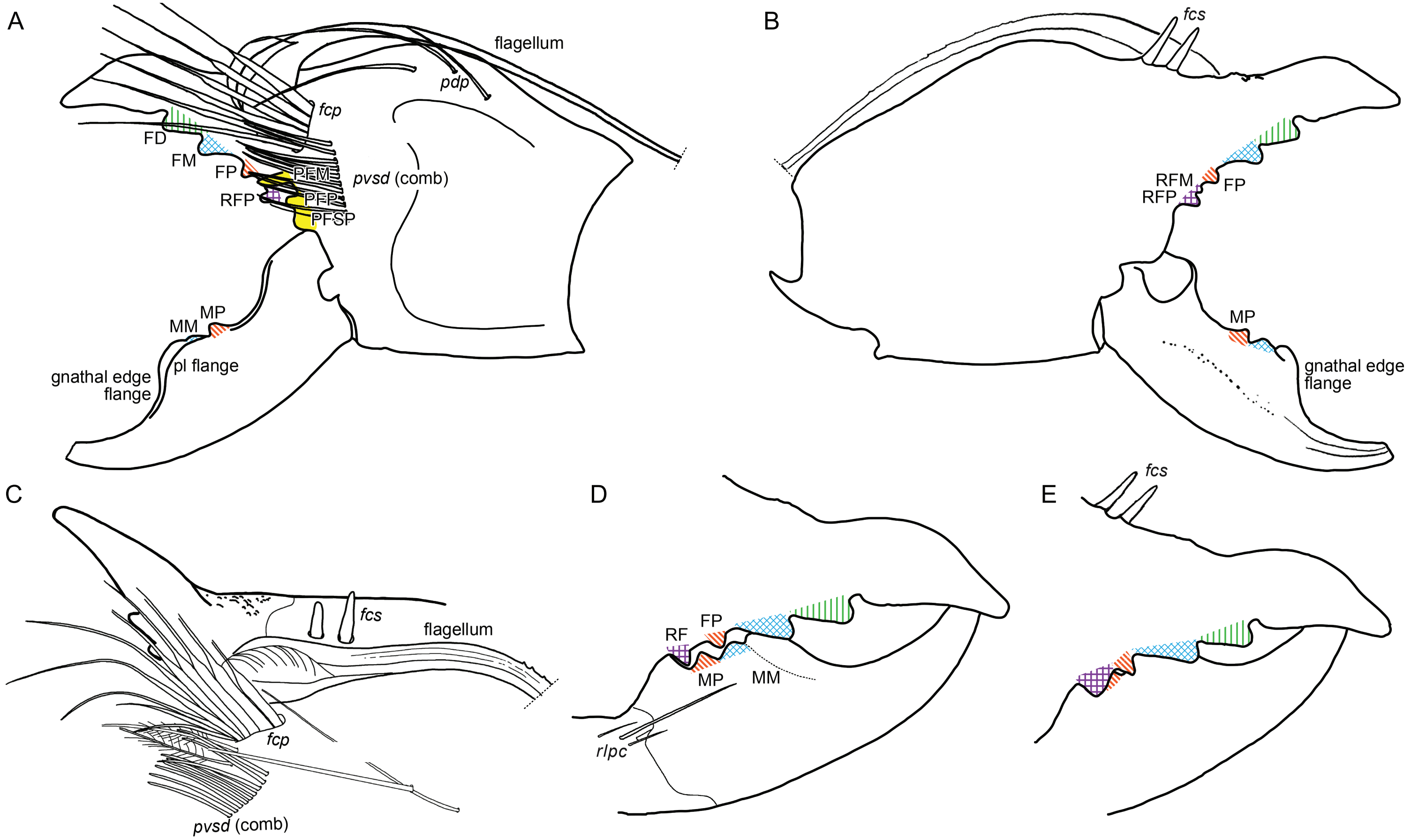

A
flagellum
pdp
fcp
FD
FM
FP
PFM
pvsd (comb)
RFP
PFP
PFSP
MM
MP
pl flange
gnathal edge flange
B
fcs
RFM
RFP
FP
MP
gnathal edge flange
C
fcs
flagellum
fcp
pvsd (comb)
D
FP
RF
MP
MM
rlpc
E
fcs

PLATE 93. Ceromidae Roewer, 1933, *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106), chelicerae, prolateral (**A**) and retrolateral (**B, D, E**) views, and fixed finger, prodorsal view (**C**), illustrating setae and flagellar complex. Abbreviations: ***fcp*,** flagellum complex plumose setae (modified proventral distal setae, or *pvd*); ***fcs*,** flagellar complex spiniform setae (modified prodorsal distal setae, or *pdd*); **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **pl,** prolateral; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

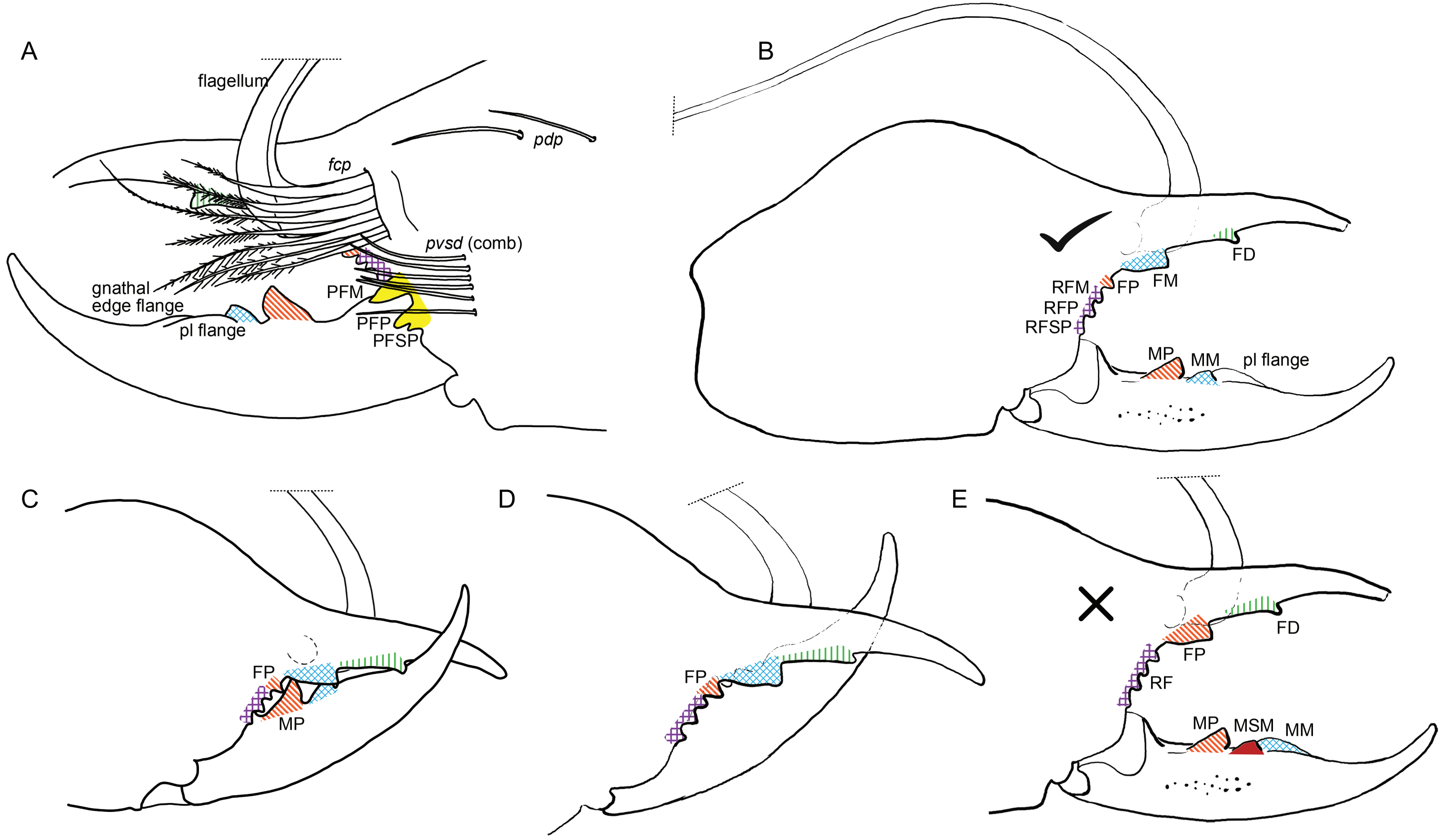

A
flagellum
pdp
fcp
pvsd (comb)
gnathal edge flange
pl flange
PFM
PFP
PFSP
B
FD
FM
FP
RFM
RFP
RFSP
MP
MM
pl flange
C
FP
MP
D
FP
E
FD
FP
RF
MP
MSM
MM

PLATE 94. Ceromidae Roewer, 1933, *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355), chelicerae, prolateral (**A**) and retrolateral (**B–E**) views, illustrating movable finger interpretations of dentition by previous authors (Lawrence, 1935b; Roewer, 1941), indicated by X (**E**), and proposed here, indicated by check mark (**B**), setae, and flagellar complex. Abbreviations: ***fcp*,** flagellum complex plumose setae (modified proventral distal setae, or *pvd*); **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **pl,** prolateral; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth.

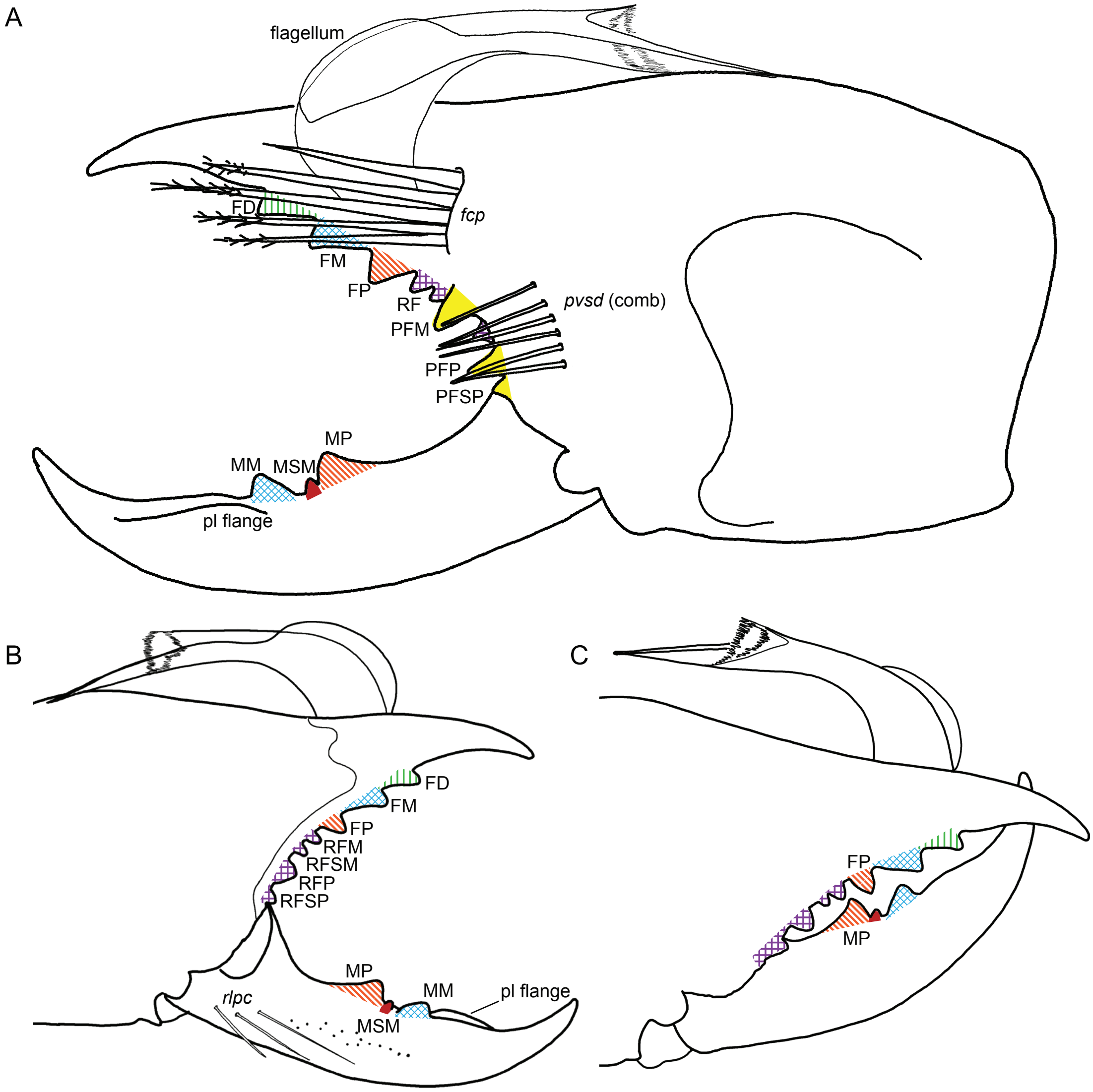

A
flagellum
fcp
FD
FM
FP
RF
PFM
pvsd (comb)
PFP
PFSP
MP
MM
MSM
pl flange
B
FD
FM
FP
RFM
RFSM
RFP
RFSP
MP
rlpc
MM
pl flange
MSM
C
FP
MP

PLATE 95. Ceromidae Roewer, 1933, *Ceromella* sp., ♂ (AMNH [LP 8527]), chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellar complex. Abbreviations: ***fcp*,** flagellum complex plumose setae (modified proventral distal setae, or *pvd*); **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **pl,** prolateral; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

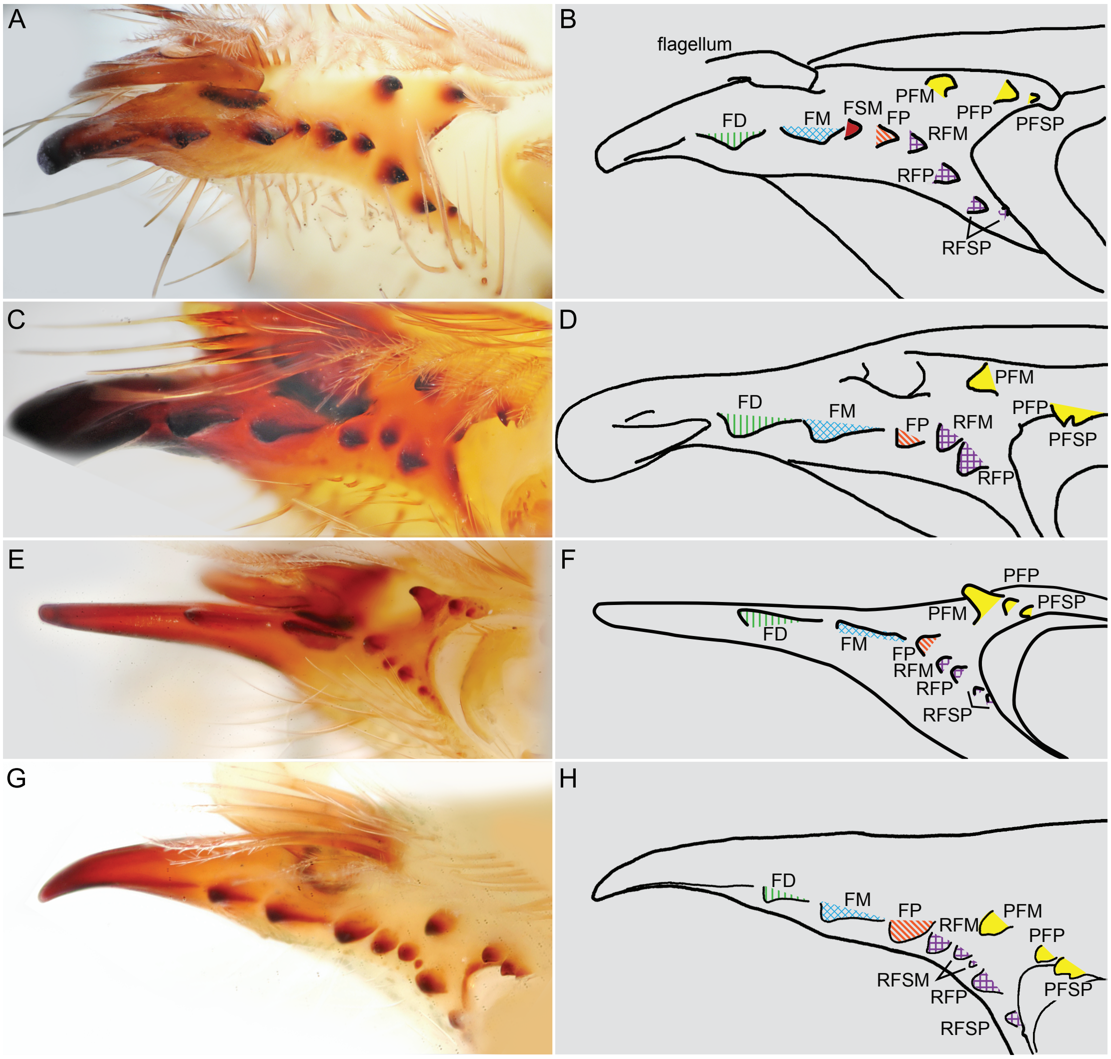

A
B
flagellum
PFM
FD
FM
FSM
FP
PFP
PFSP
RFM
RFP
RFSP
C
D
PFM
FD
FM
FP
RFM
PFP
PFSP
RFP
E
F
PFP
PFSP
PFM
FD
FM
FP
RFM
RFP
RFSP
G
H
FD
FM
FP
RFM
PFM
PFP
PFSP
RFSM
RFP
RFSP

PLATE 96. Ceromidae Roewer, 1933, cheliceral fixed fingers, proventral views illustrating fondal area. **A, B.** *Ceroma inerme* Purcell, 1899, ♂ (AMNH [LP 9864]). **C, D.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **E, F.** *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355). **G, H.** *Ceromella* sp., ♂ (AMNH [LP 8527]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial teeth; **RFSP,** retrofondal subproximal teeth.

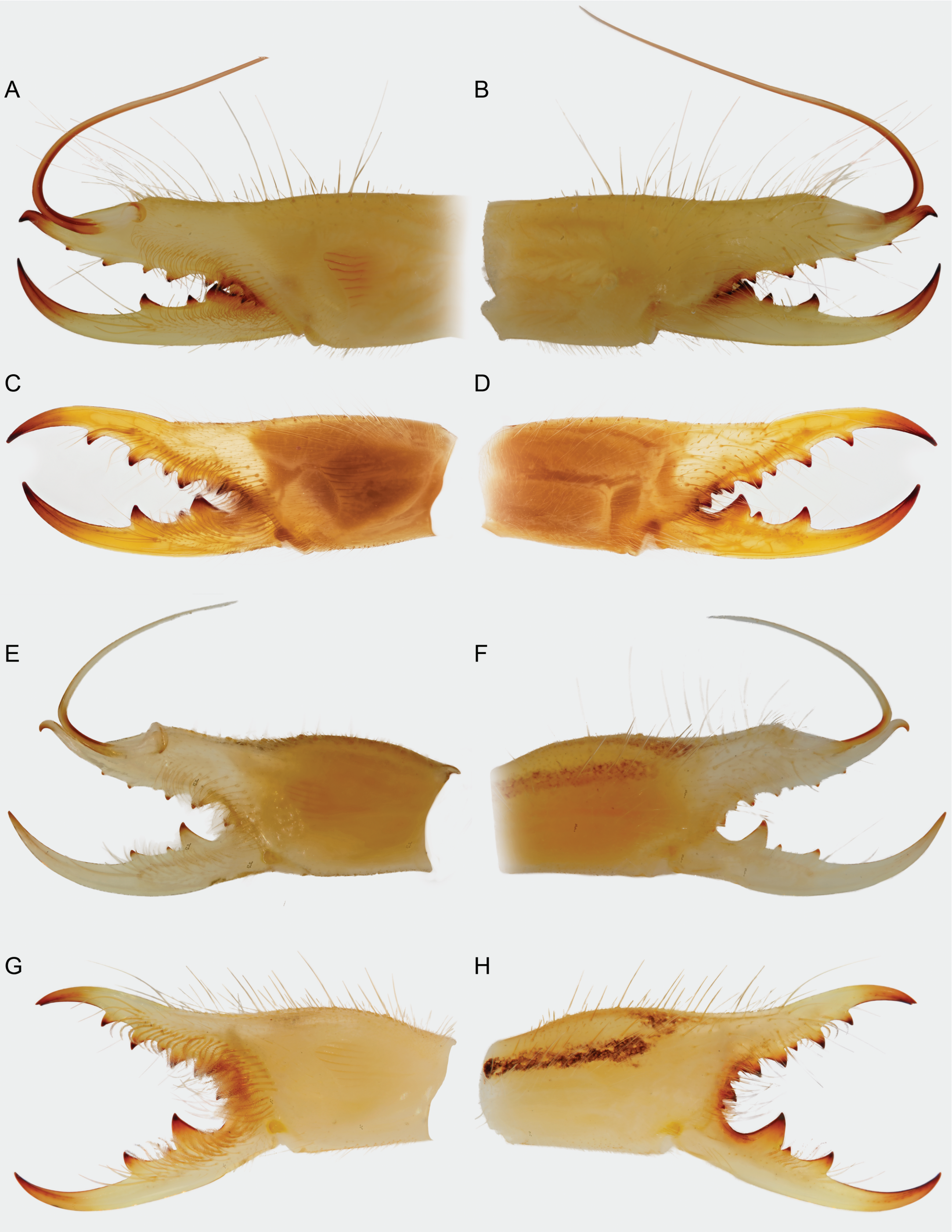


PLATE 97. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A–D.** *Metasolpuga picta* (Kraepelin, 1899). **A, B.** ♂ (AMNH [LP 10719]). **C, D.** subad. ♂ (AMNH), Namibia: Gobabeb. **E–H.** *Prosolpuga schultzei* (Kraepelin, 1908). **E, F.** ♂ (NMNW 13759). **G, H.** ♀ (AMNH [LP 3605]).

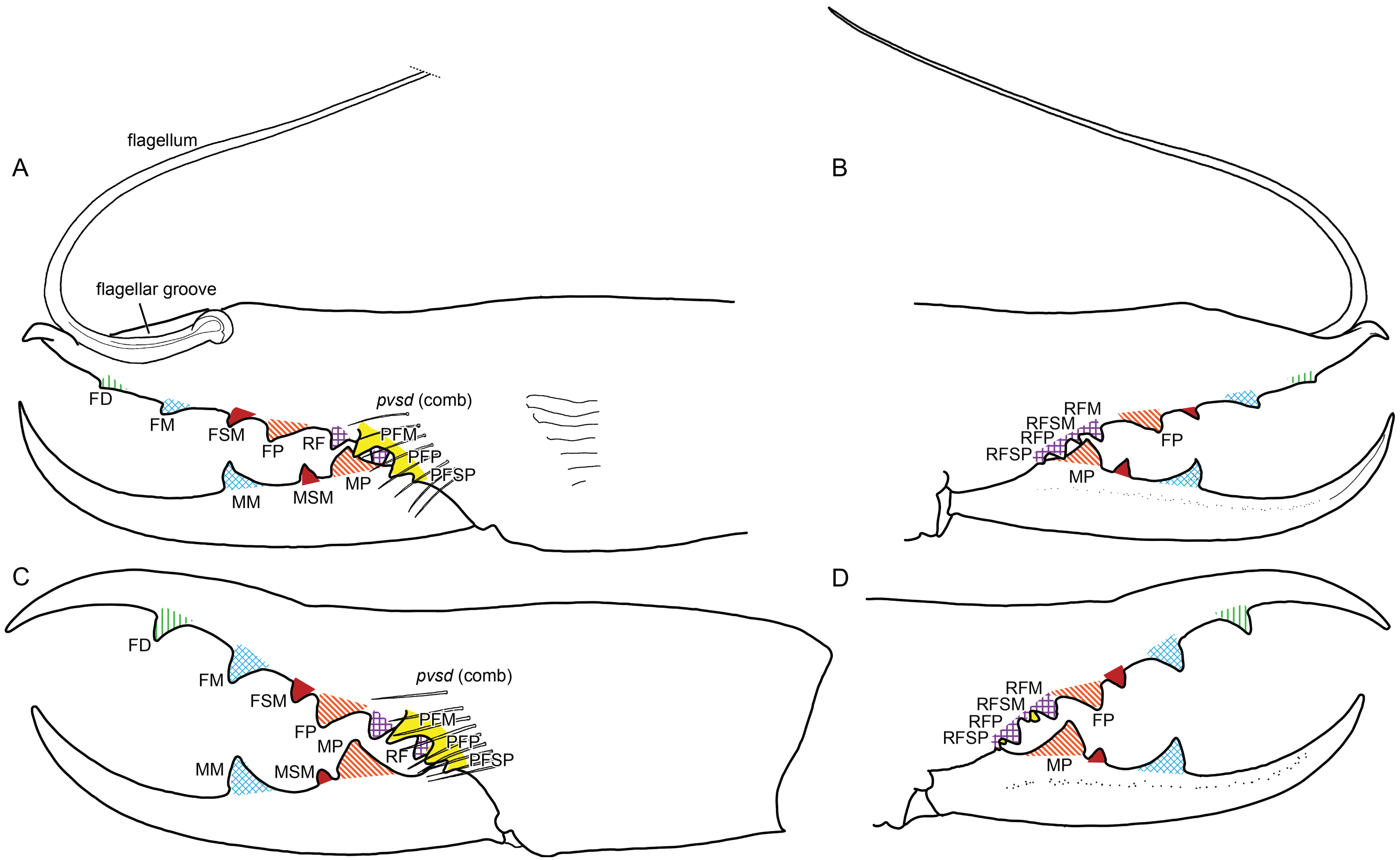

A
flagellum
flagellar groove
FD
FM
FSM
FP
RF
pvsd (comb)
PFM
PFP
PFSP
MM
MSM
MP
B
RFM
RFSM
RFP
RFSP
FP
MP
C
FD
FM
FSM
FP
MP
RF
pvsd (comb)
PFM
PFP
PFSP
MM
MSM
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 98. Solpugidae Leach, 1815, *Metasolpuga picta* (Kraepelin, 1899), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 10719]). **C, D.** subad. ♂ (AMNH), Namibia: Gobabeb. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd,*** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

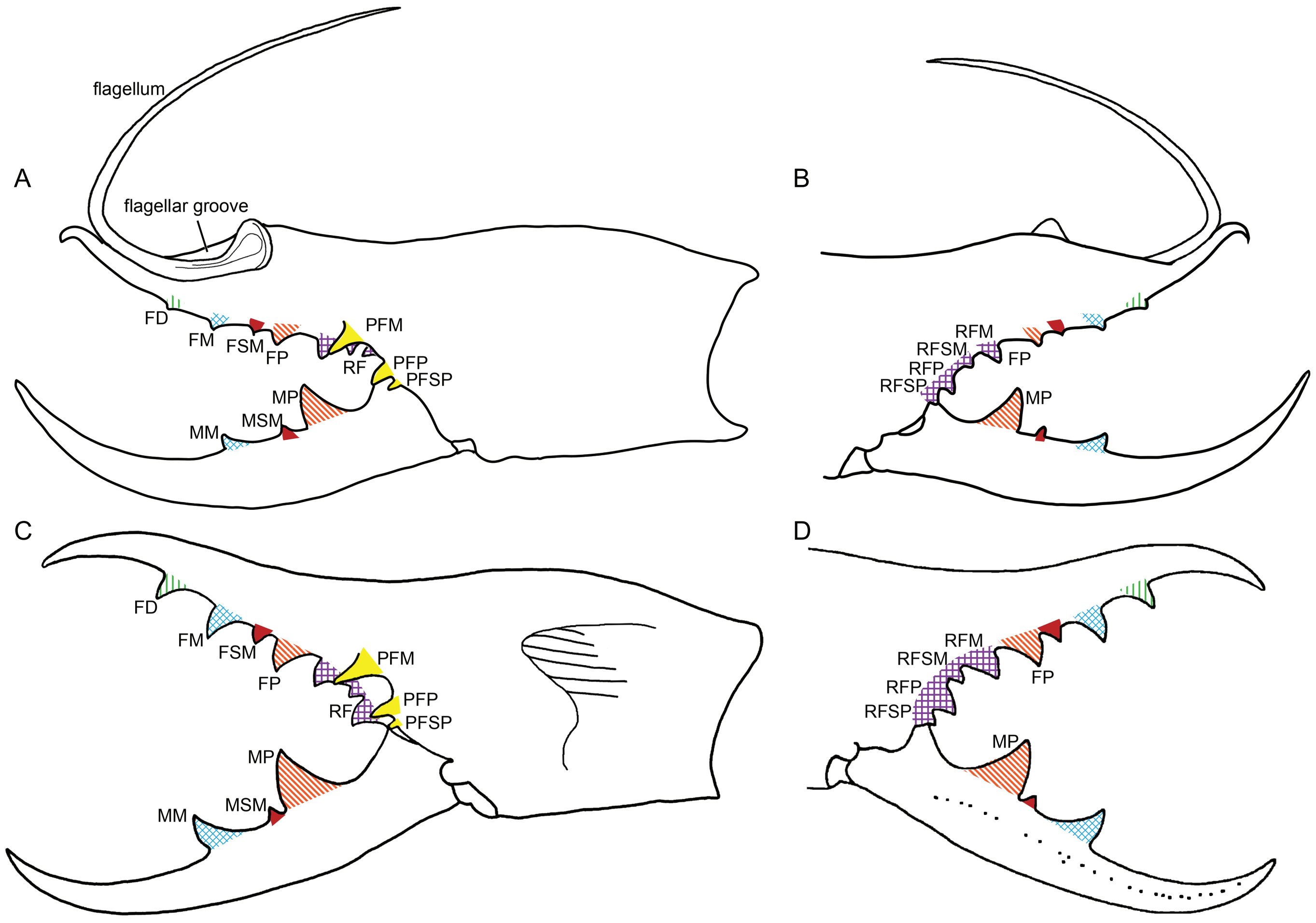

A
flagellum
flagellar groove
FD
FM
FSM
FP
PFM
RF
PFP
PFSP
MP
MSM
MM
B
RFM
RFSM
RFP
RFSP
FP
MP
C
FD
FM
FSM
FP
PFM
RF
PFP
PFSP
MP
MSM
MM
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 99. Solpugidae Leach, 1815, *Prosolpuga schultzei* (Kraepelin, 1908), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (NMNW 13759). **C, D.** ♀ (AMNH [LP 3605]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal teeth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

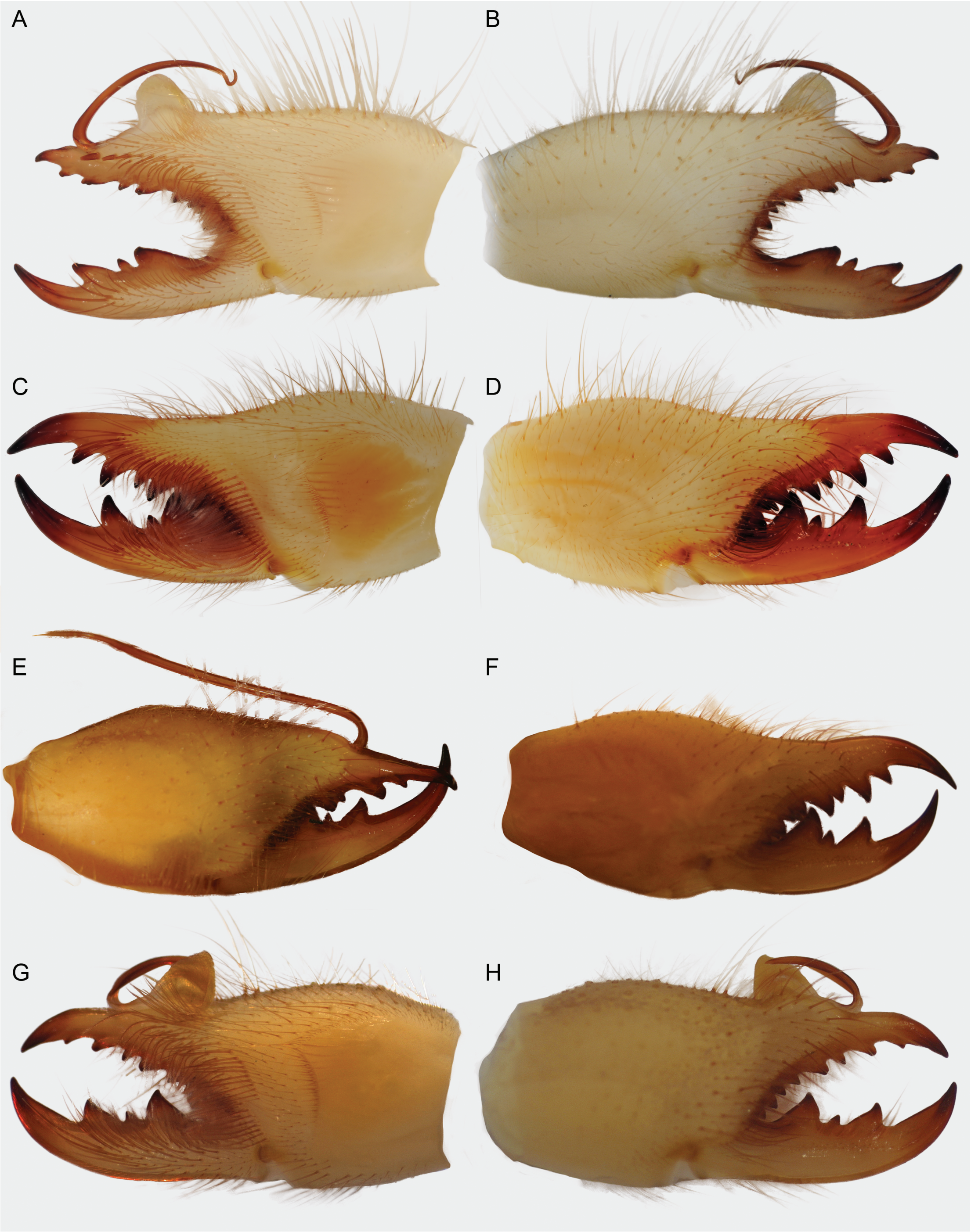


PLATE 100. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, G**) and retrolateral (**B, D–F, H**) views. **A–D.** *Oparba asiatica* (Turk, 1948). **A, B.** ♂ (HUJI 684). **C, D.** ♀ (TAUZM 50313). **E, F.** *Oparbella flavescens* (C.L. Koch, 1842). **E.** ♂ (MCZ 102912). **F.** ♀ (MCZ 102912). **G, H.** *Oparbella* sp., ♂ (MRAC 230.211).

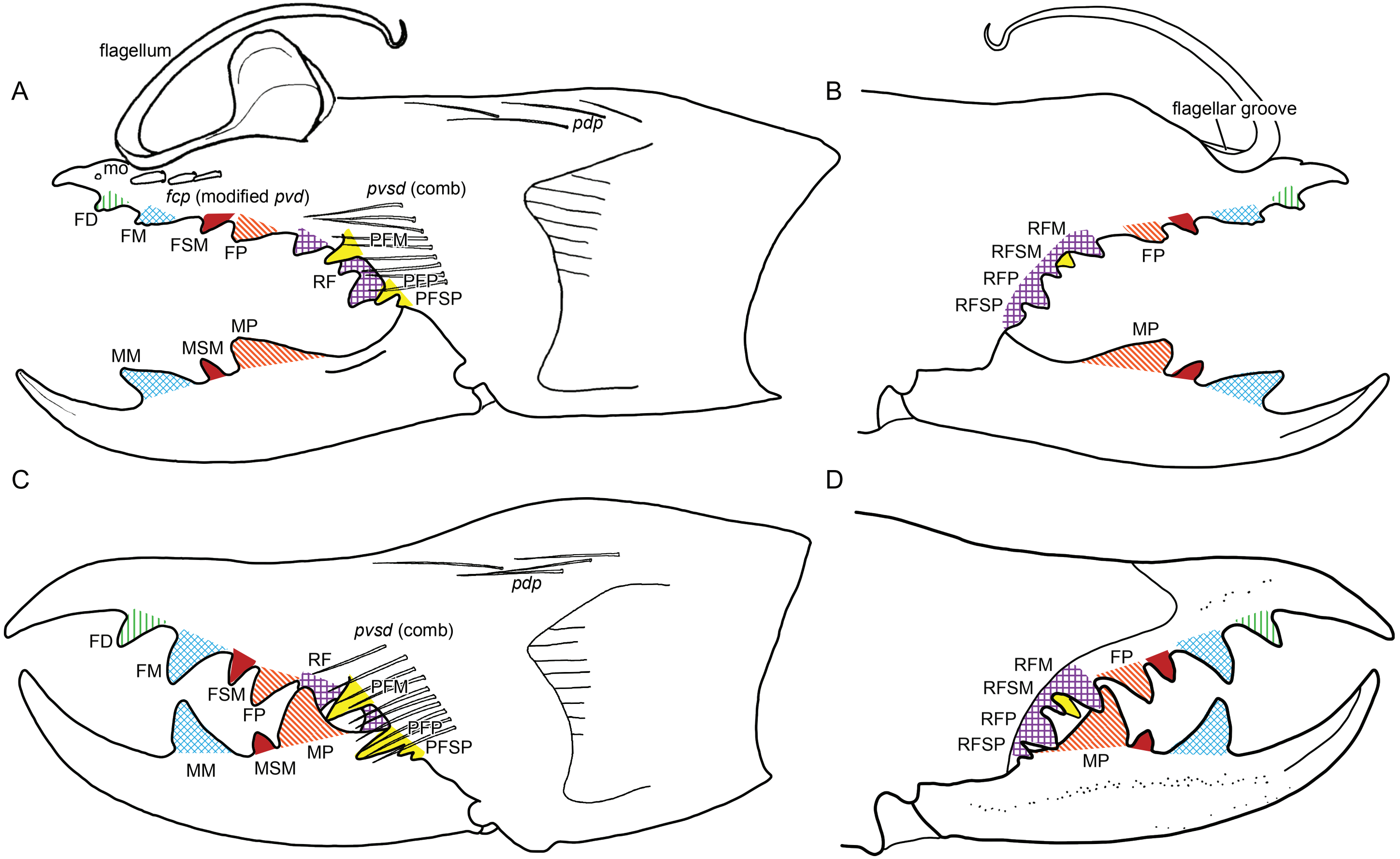

A
flagellum
mo
fcp (modified pvd)
pvsd (comb)
pdp
FD
FM
FSM
FP
PFM
RF
PFP
PFSP
MM
MSM
MP
B
flagellar groove
RFM
RFSM
RFP
RFSP
FP
MP
C
pdp
pvsd (comb)
FD
FM
FSM
FP
RF
PFM
PFP
PFSP
MM
MSM
MP
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 101. Solpugidae Leach, 1815, *Oparba asiatica* (Turk, 1948), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (HUJI 684). **C, D.** ♀ (TAUZM 50313). Abbreviations: ***fcp*,** flagellar complex plumose setae; **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **mo,** mucron organ; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvd*,** proventral distal setae; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

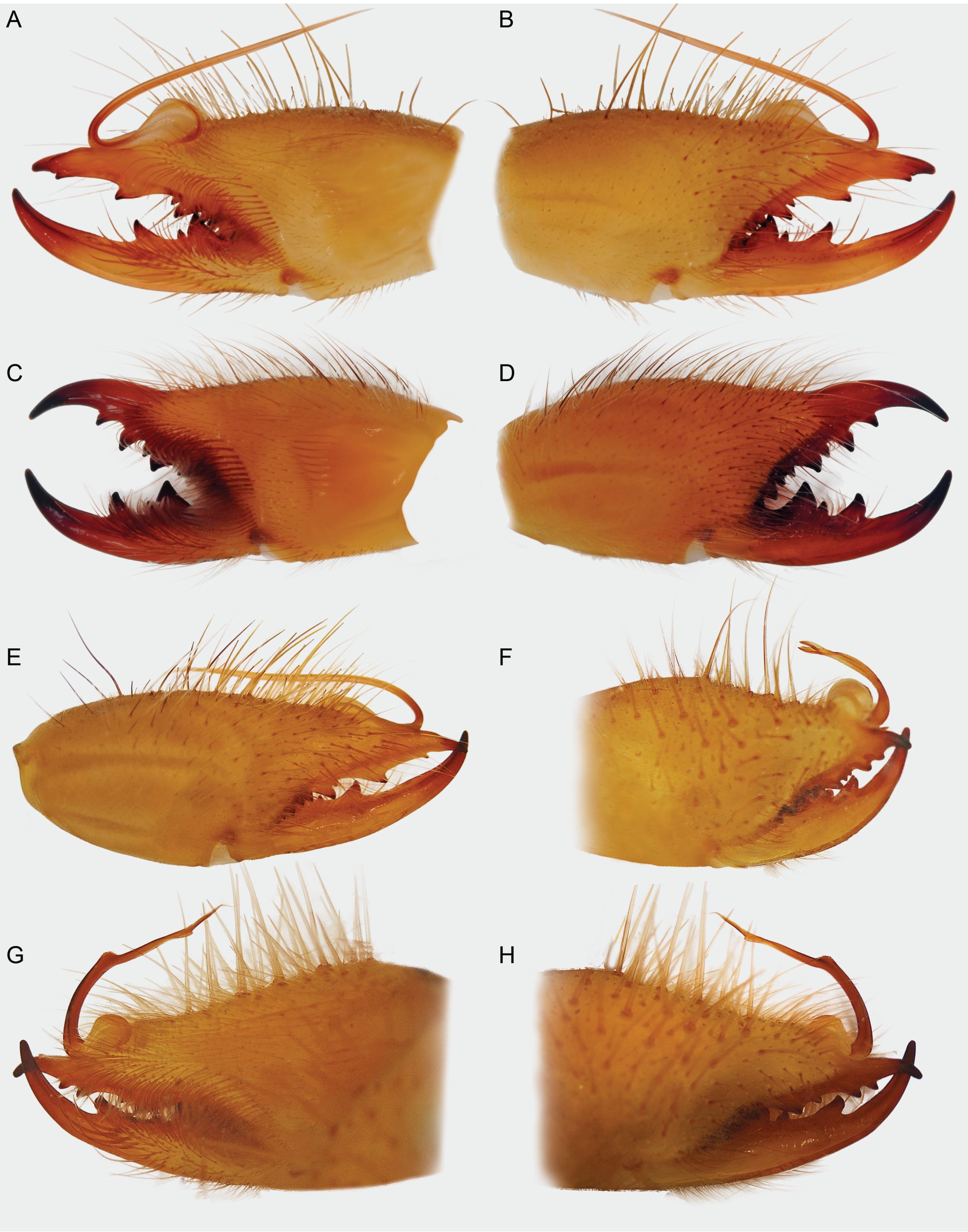


PLATE 102. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, G**) and retrolateral (**B, D–F, H**) views. **A–E.** *Solpuga chelicornis* Lichtenstein, 1796. **A, B.** ♂ (AMNH [LP 8158]). **C, D.** ♀ (NCA 2008/3524). **E.** ♂ (NCA 2008/3524). **F.** *Solpuga massaica* Roewer, 1941, ♂ (SMF [RII/7391]). **G, H.** *Solpuga roeweri* Fage, 1936, ♂ (MCZ 126317).

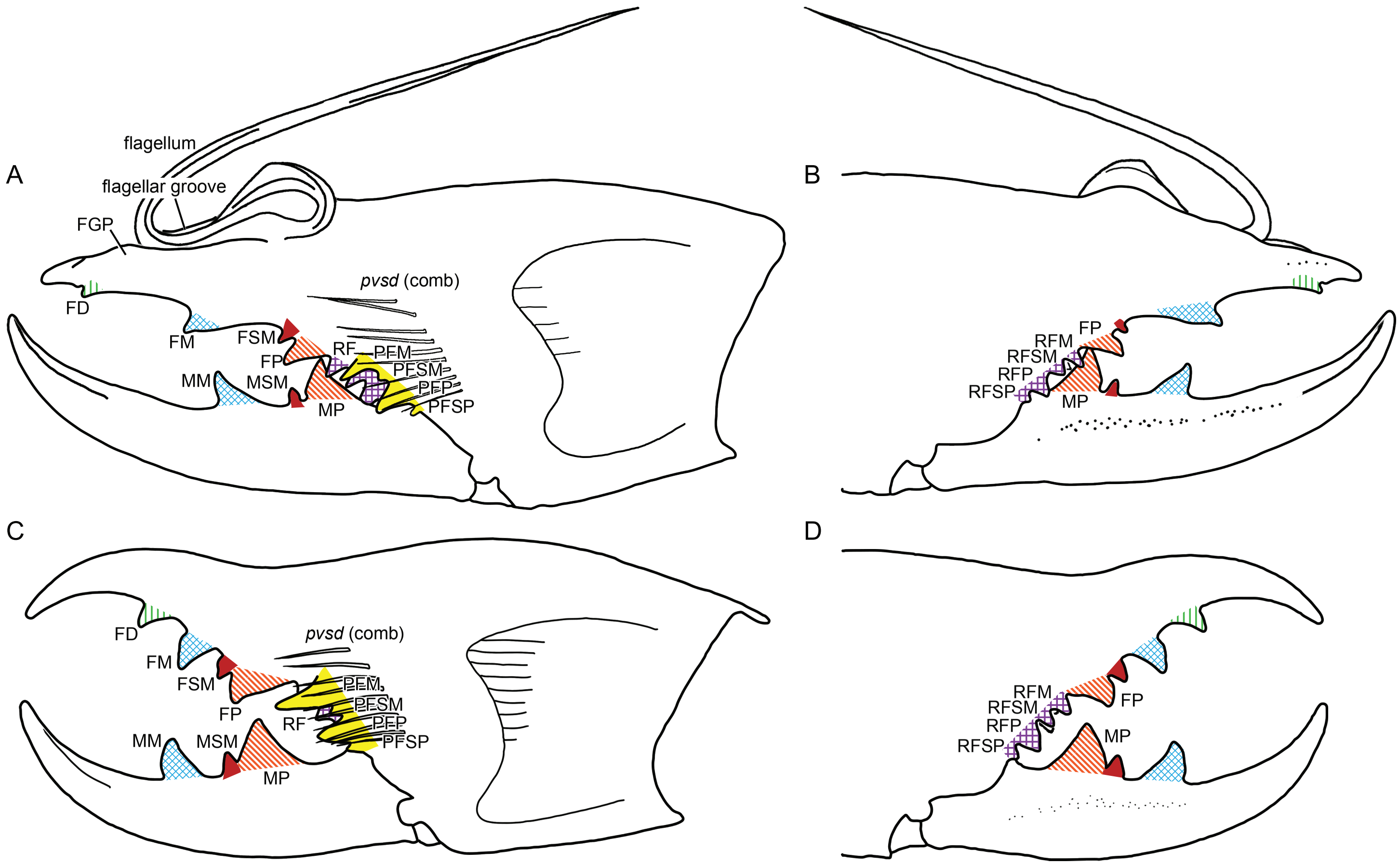

A
flagellum
flagellar groove
FGP
FD
FM
FSM
FP
MM
MSM
MP
pvsd (comb)
RF
PFM
PFSM
PFP
PFSP
B
FP
RFM
RFSM
RFP
RFSP
MP
C
FD
FM
FSM
FP
MM
MSM
MP
pvsd (comb)
RF
PFM
PFSM
PFP
PFSP
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 103. Solpugidae Leach, 1815, *Solpuga chelicornis* Lichtenstein, 1796, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 8158]). **C, D.** ♀ (NCA 2008/3524). Abbreviations: **FD,** fixed finger, distal tooth; **FGP,** flagellar groove process; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

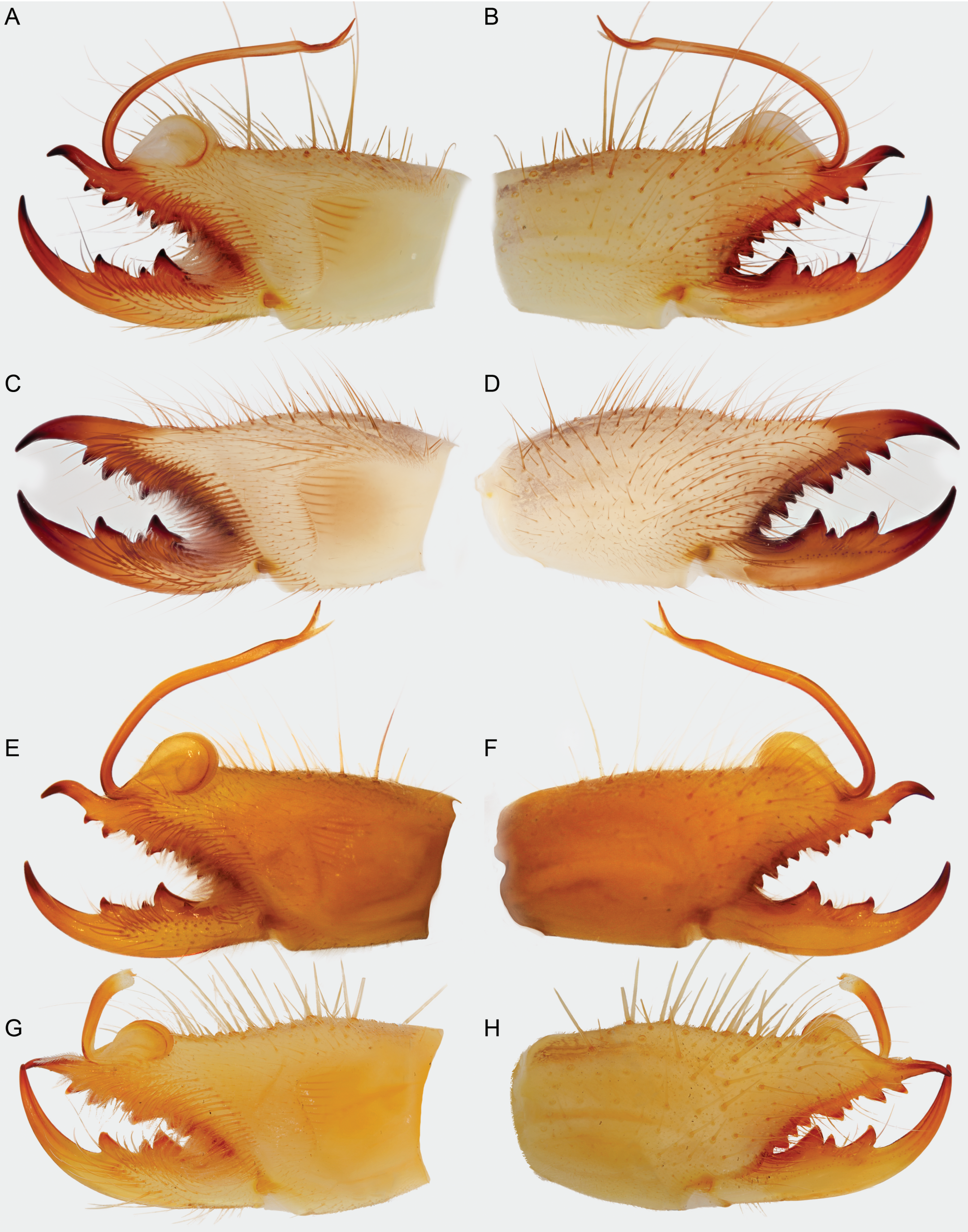


PLATE 104. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A–D.** *Solpugassa furcifera* (Kraepelin, 1899). **A, B.** ♂ (AMNH [LP 3632]). **C, D.** ♀ (AMNH [LP 3632]). **E, F.** *Solpugassa furcifera* (Kraepelin, 1899), holotype ♂ (TMSA 8843) [*Solpugassa kochi* Lawrence, 1959]. **G, H.** *Solpugella* sp., ♂ (NMNW 11097).

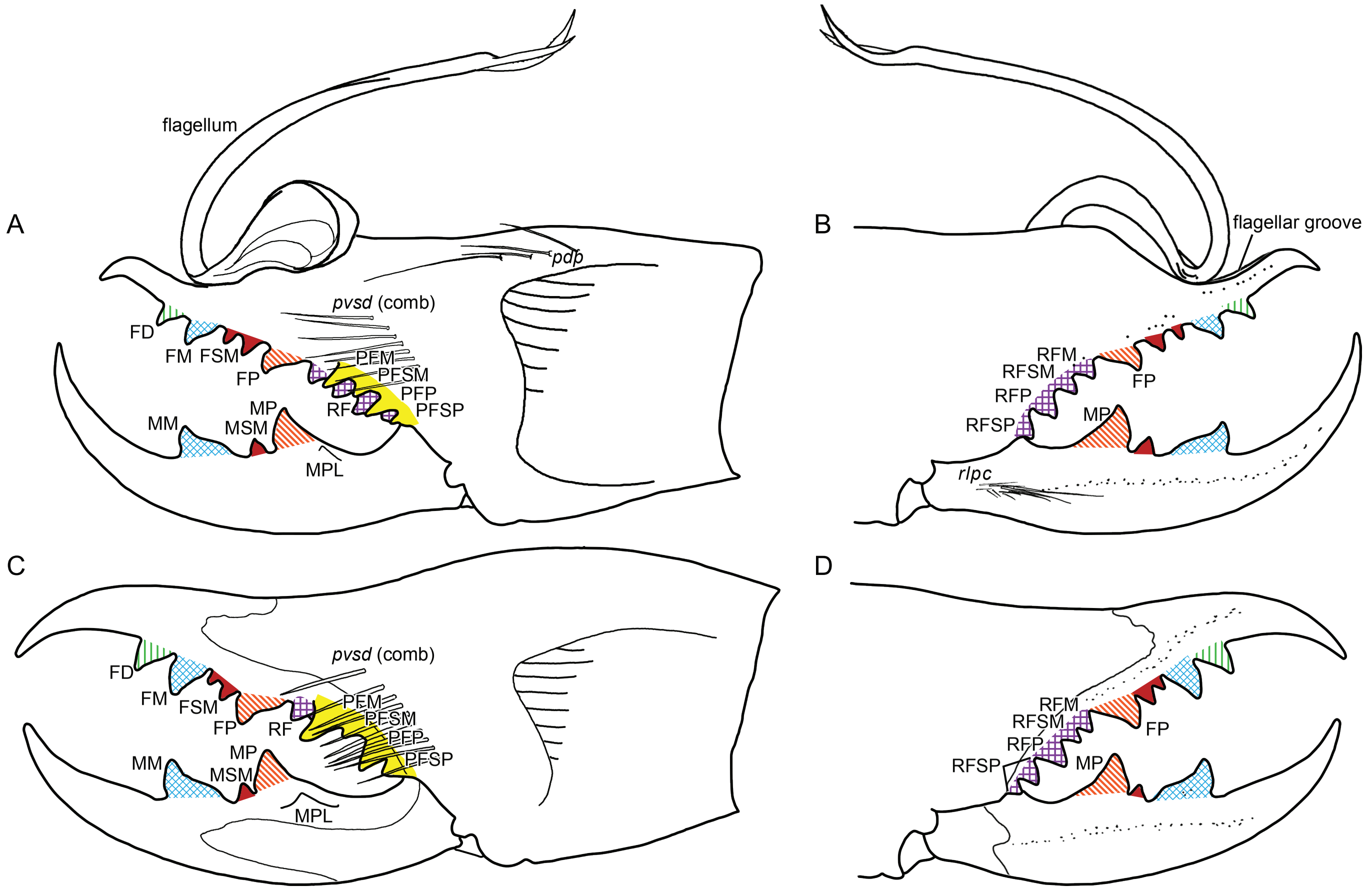

A
flagellum
pdp
pvsd (comb)
FD
FM FSM
FP
PFM
PFSM
PFP
PFSP
RF
MM
MP
MSM
MPL
B
flagellar groove
RFM
RFSM
RFP
RFSP
FP
MP
rlpc
C
pvsd (comb)
FD
FM
FSM
FP
RF
PFM
PFSM
PFP
PFSP
MM
MP
MSM
MPL
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 105. Solpugidae Leach, 1815, *Solpugassa furcifera* (Kraepelin, 1899), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 3632]). **C, D.** ♀ (AMNH [LP 3632]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MSM,** movable finger, submedial tooth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

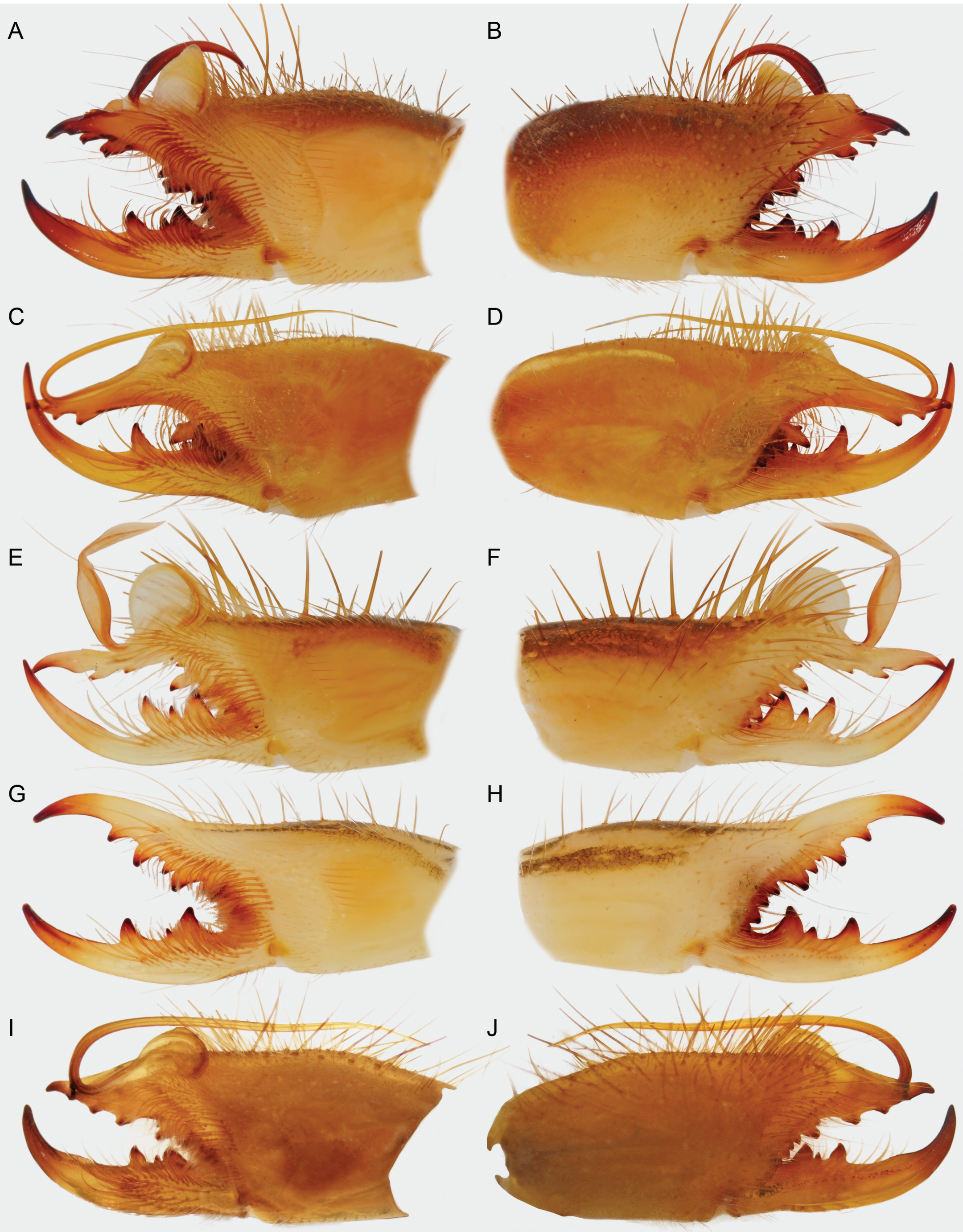


PLATE 106. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). **C, D.** *Solpugema derbiana* (Pocock, 1895), ♂ (AMNH [LP 7709]). **E–H.** *Solpugema genucornis* (Lawrence, 1935). **E, F.** ♂ (AMNH [LP 8167]). **G, H.** ♀ (AMNH [LP 10292]). **I, J.** *Solpugema hamata* (Hewitt, 1914), ♂ (TMSA 6632).

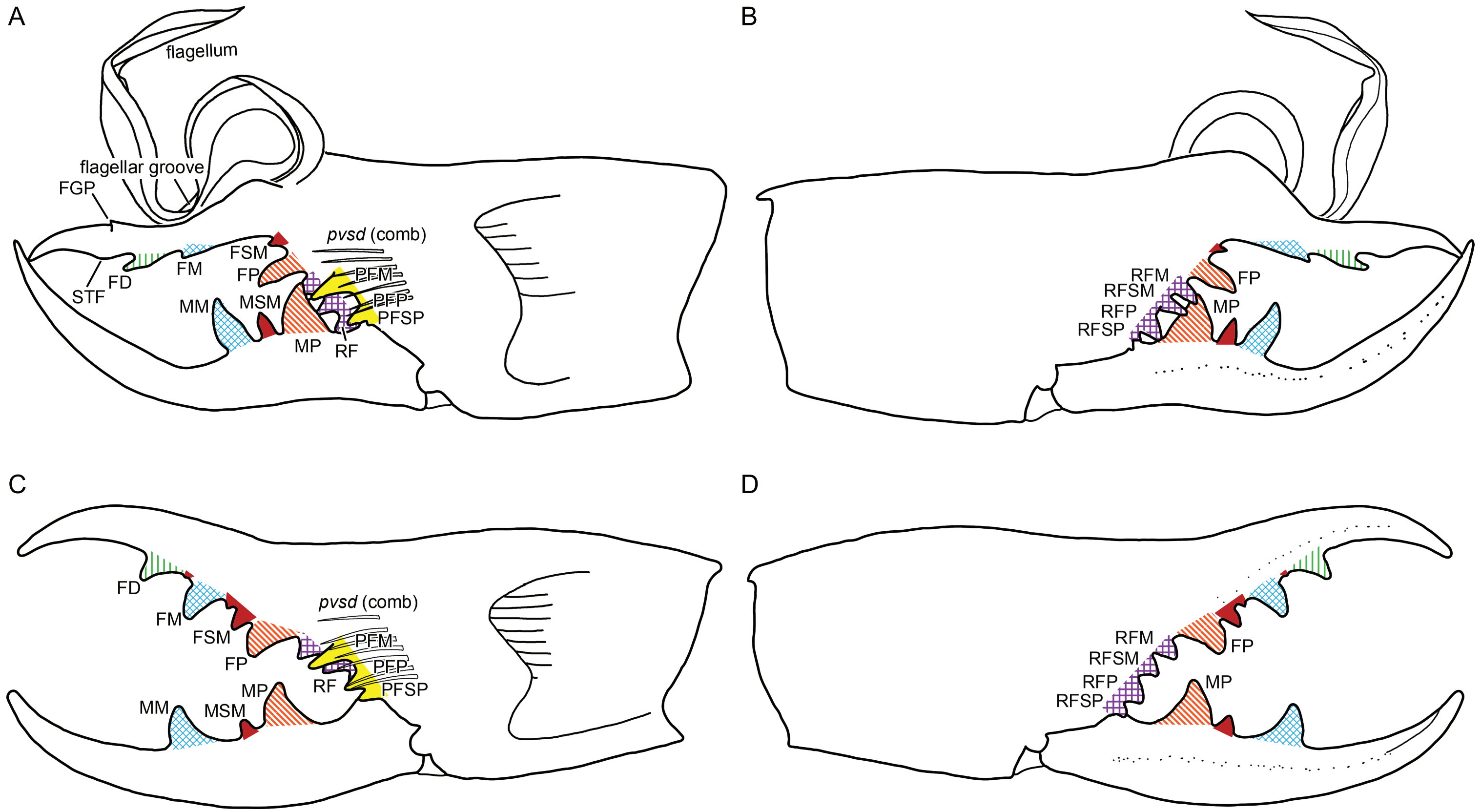

A
flagellum
flagellar groove
FGP
STF
FD
FM
FSM
FP
MM
MSM
MP
RF
pvsd (comb)
PFM
PFP
PFSP
B
RFM
RFSM
RFP
RFSP
FP
MP
C
FD
FM
FSM
FP
MM
MSM
MP
RF
pvsd (comb)
PFM
PFP
PFSP
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 107. Solpugidae Leach, 1815, *Solpugema genucornis* (Lawrence, 1935), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 8167]). **C, D.** ♀ (AMNH [LP 10292]). Abbreviations: **FD,** fixed finger, distal tooth; **FGP,** flagellar groove process; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; **STF,** subterminal flange.

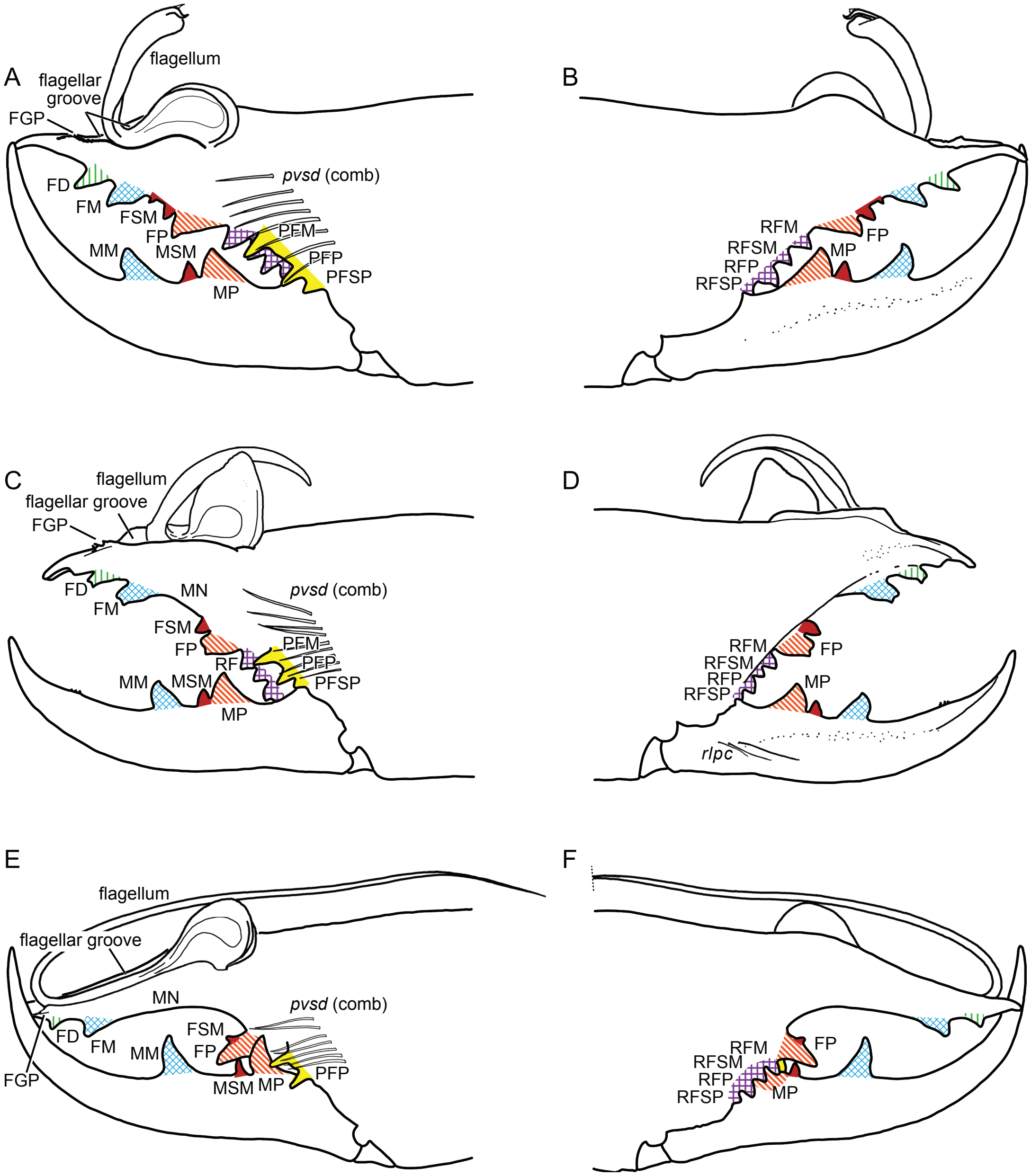

A
flagellum
flagellar groove
FGP
FD
FM
FSM
FP
MM
MSM
MP
pvsd (comb)
PFM
PFP
PFSP
B
RFM
RFSM
RFP
RFSP
FP
MP
C
flagellum
flagellar groove
FGP
FD
FM
MN
FSM
FP
RF
MM
MSM
MP
pvsd (comb)
PFM
PFP
PFSP
D
RFM
RFSM
RFP
RFSP
FP
MP
rlpc
E
flagellum
flagellar groove
MN
FD
FM
MM
FSM
FP
FGP
MSM
MP
pvsd (comb)
PFP
F
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 108. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D, F**) views, illustrating dentition, setae, and male flagellum. **A, B.** *Solpugella* sp., ♂ (NMNW 11097). **C, D.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). **E, F.** *Solpugema derbiana* (Pocock, 1895), ♂ (AMNH [LP 7709]). Abbreviations: **FD,** fixed finger, distal tooth; **FGP,** flagellar groove process; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MN,** medial notch; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

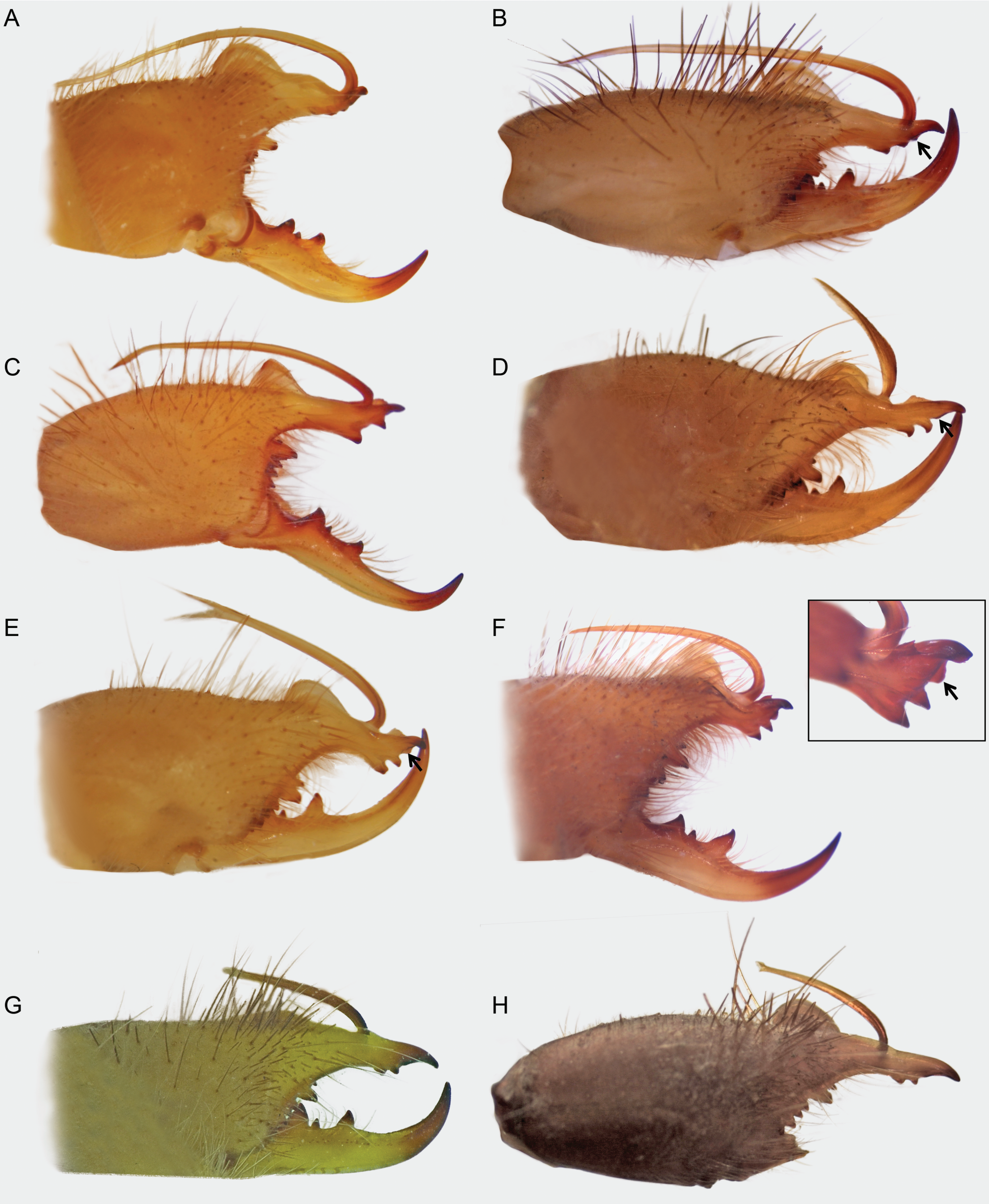


PLATE 109. Solpugidae Leach, 1815, chelicerae, retrolateral views. **A, B.** *Solpugema hostilis* (White, 1846). **A.** ♂ (SMF [R3117]). **B.** ♂ (NCA 2009/2817). **C.** *Solpugema* sp., ♂ (NCA 97/821). **D.** *Solpugema phylloceras* (Lawrence, 1929), ♂ (TMSA 8606). **E.** *Solpugema montana* (Lawrence, 1929), ♂ (SMF [RII/2904]). **F.** *Solpugema intermedia* (Lawrence, 1929), ♂ (NCA 2009/4482). Inset: Distal part of fixed (dorsal) finger. **G, H.** *Solpugema tubicen* (Kraepelin, 1911). **G.** Syntype ♂ (ZMUH [R9503]), **H.** ♂ (TMSA 2643). Arrows indicate subterminal flange (STF).

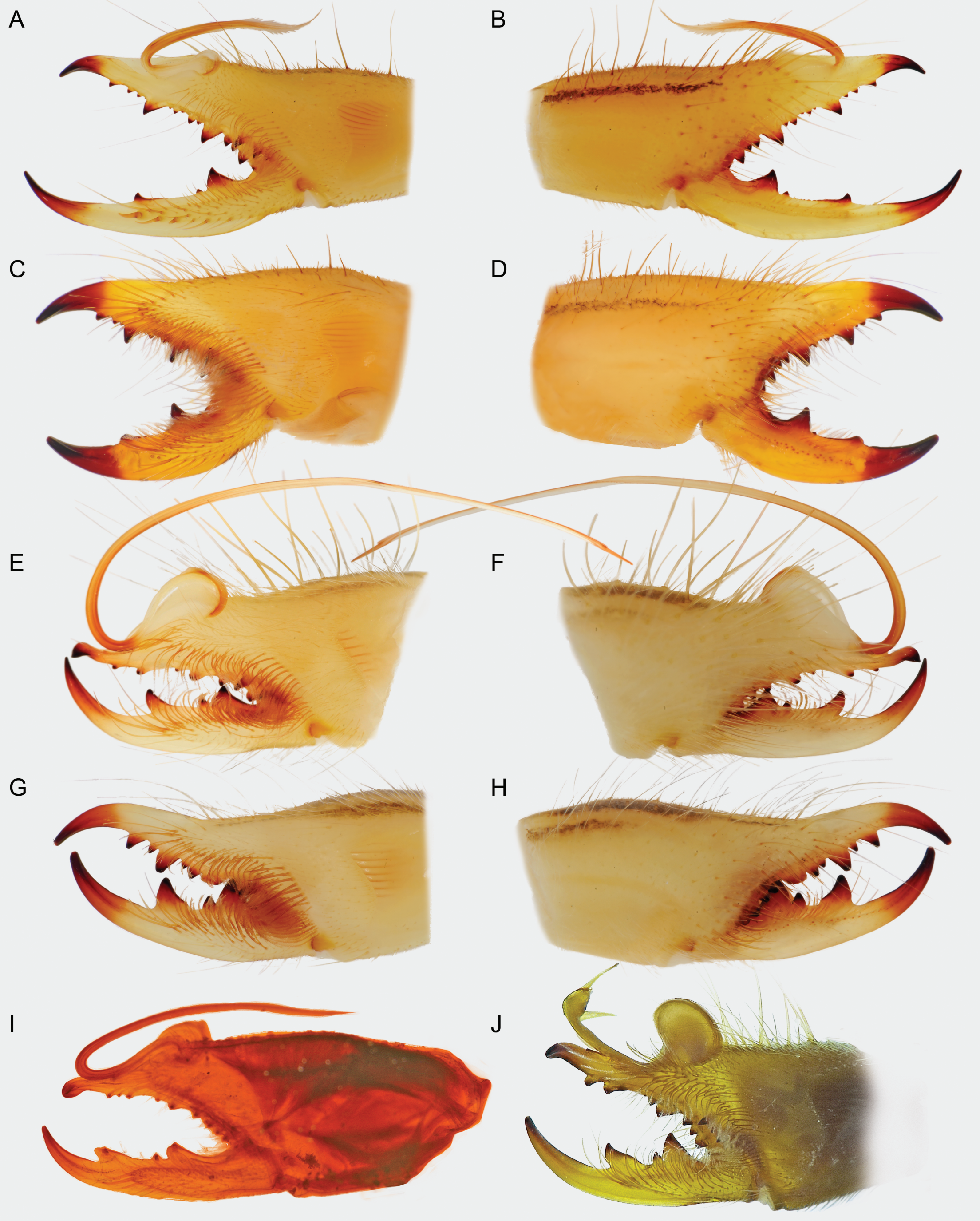


PLATE 110. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G, I, J**) and retrolateral (**B, D, F, H**) views. **A–D.** *Solpugiba lineata* (C.L. Koch, 1842). **A, B.** ♂ (AMNH [LP 5919]). **C, D.** ♀ (AMNH [LP 5919]). **E–H.** *Solpugista bicolor* (Lawrence, 1953). **E, F.** ♂ (AMNH [LP 7933]). **G, H.** ♀ (AMNH [LP 9879]). **I.** *Solpugista hastata* (Kraepelin, 1899), holotype ♂ (SMF R6918). **J.** *Solpuguna alcicornis* (Kraepelin, 1914), syntype ♂ (ZMUH [R8515]).

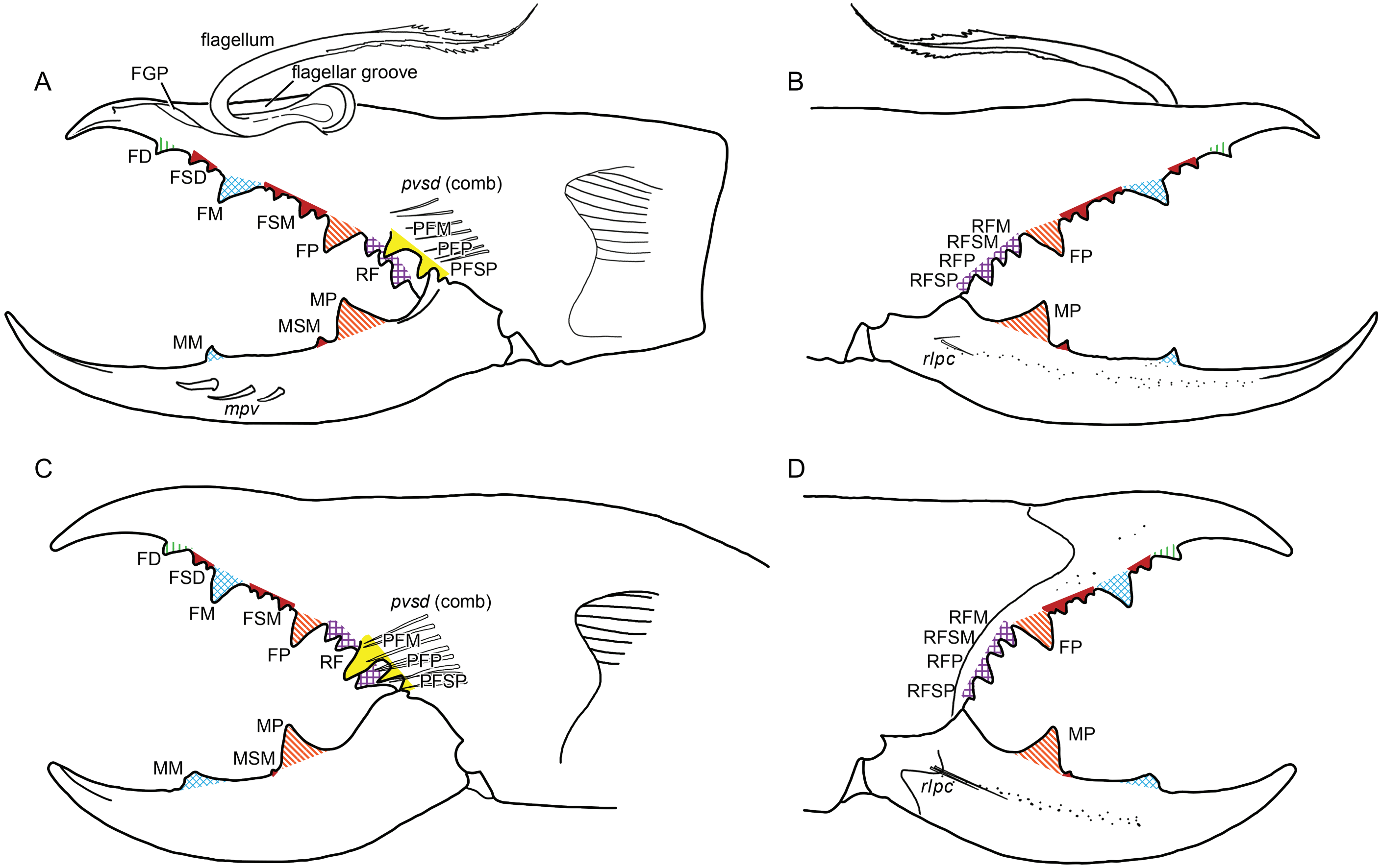

A
flagellum
FGP
flagellar groove
FD
FSD
FM
FSM
FP
pvsd (comb)
PFM
PFP
PFSP
RF
MP
MSM
MM
mpv
B
RFM
RFSM
RFP
RFSP
FP
MP
rlpc
C
FD
FSD
FM
FSM
FP
RF
pvsd (comb)
PFM
PFP
PFSP
MP
MSM
MM
D
RFM
RFSM
RFP
RFSP
FP
MP
rlpc

PLATE 111. Solpugidae Leach, 1815, *Solpugiba lineata* (C.L. Koch, 1842), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and male flagellum. **A, B.** ♂ (AMNH [LP 5919]). **C, D.** ♀ (AMNH [LP 5919]). Abbreviations: **FD,** fixed finger, distal tooth; **FGP,** flagellar groove process; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***mpv*,** movable finger, proventral setae (three apicalmost *mpv* setae illustrated in **A**); **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

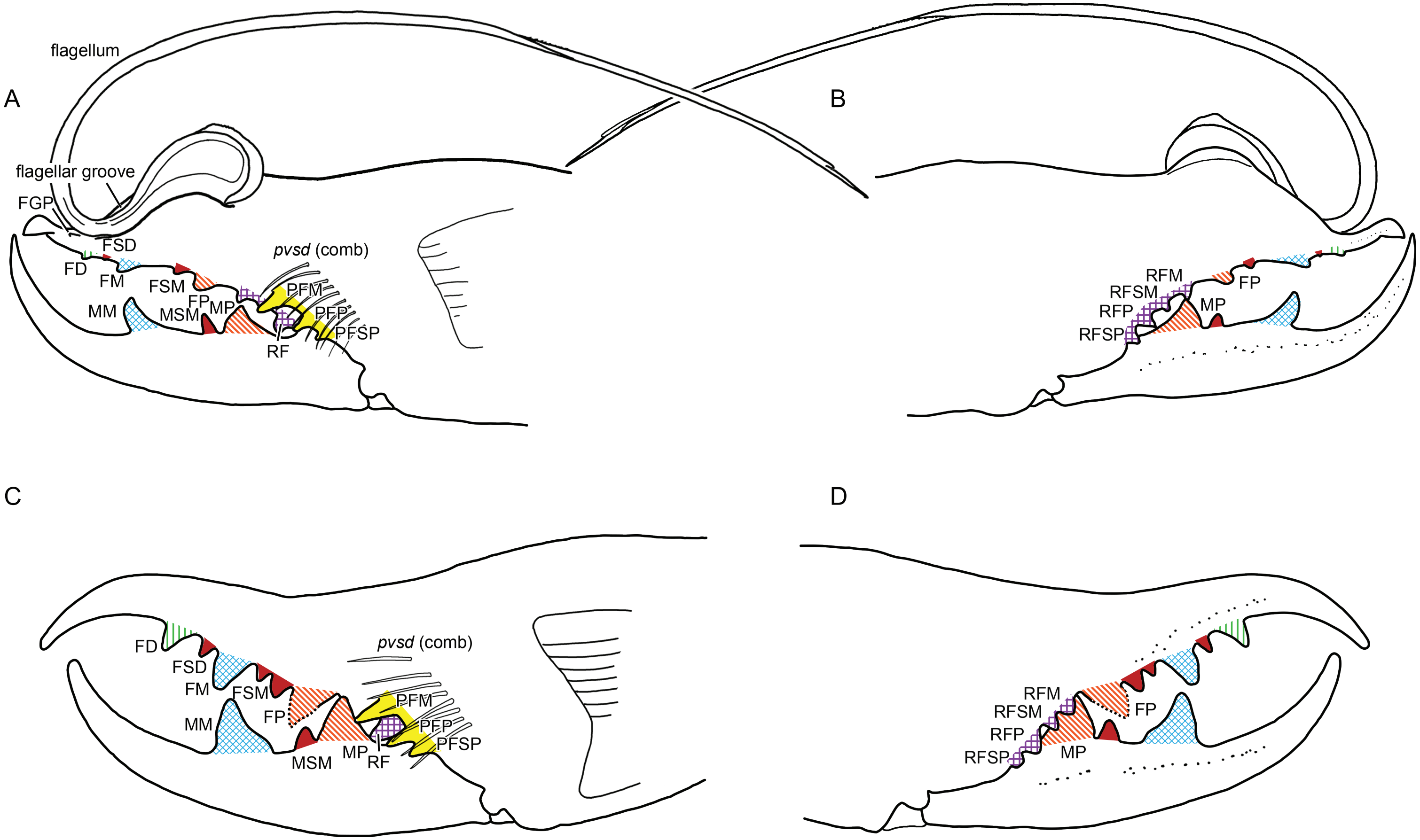

A
flagellum
flagellar groove
FGP
FSD
FD
FM
MM
FSM
MSM
FP
MP
pvsd (comb)
PFM
PFP
PFSP
RF
B
RFM
RFSM
RFP
RFSP
FP
MP
C
FD
FSD
FM
FSM
MM
FP
MSM
MP
RF
pvsd (comb)
PFM
PFP
PFSP
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 112. Solpugidae Leach, 1815, *Solpugista bicolor* (Lawrence, 1953), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 7933]). **C, D.** ♀ (AMNH [LP 9879]). Abbreviations: **FD,** fixed finger, distal tooth; **FGP,** flagellar groove process; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd,*** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

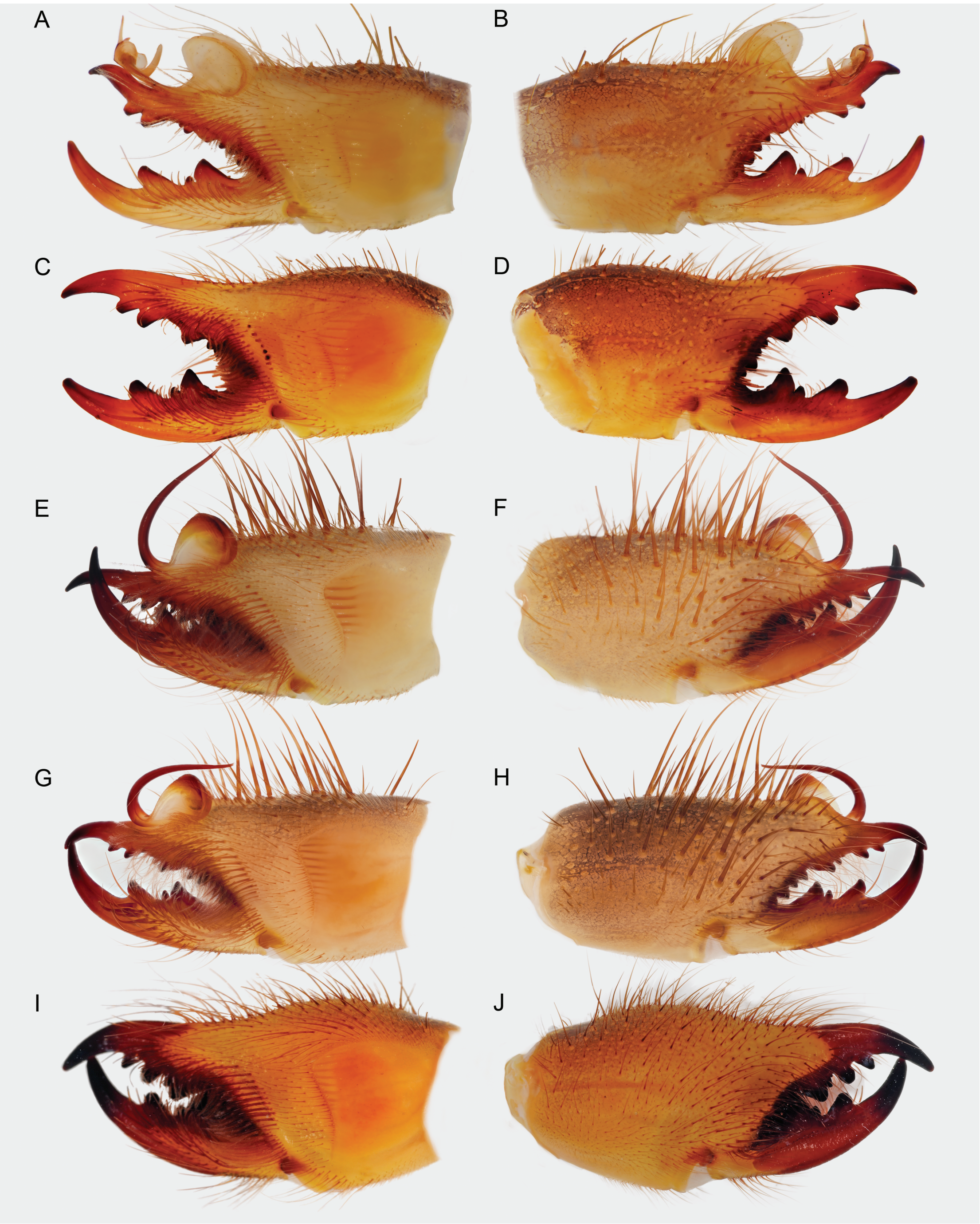


PLATE 113. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Solpuguna* cf. *orangica.* **A, B.** ♂ (AMNH [LP 5969]). **C, D.** ♀ (AMNH [LP 5969]). **E–J.** *Solpugyla* sp. **E, F.** ♂ (AMNH [LP 8138]). **G, H.** ♂ (AMNH [LP 10764]). **I, J.** ♀ (AMNH [LP 10764]).

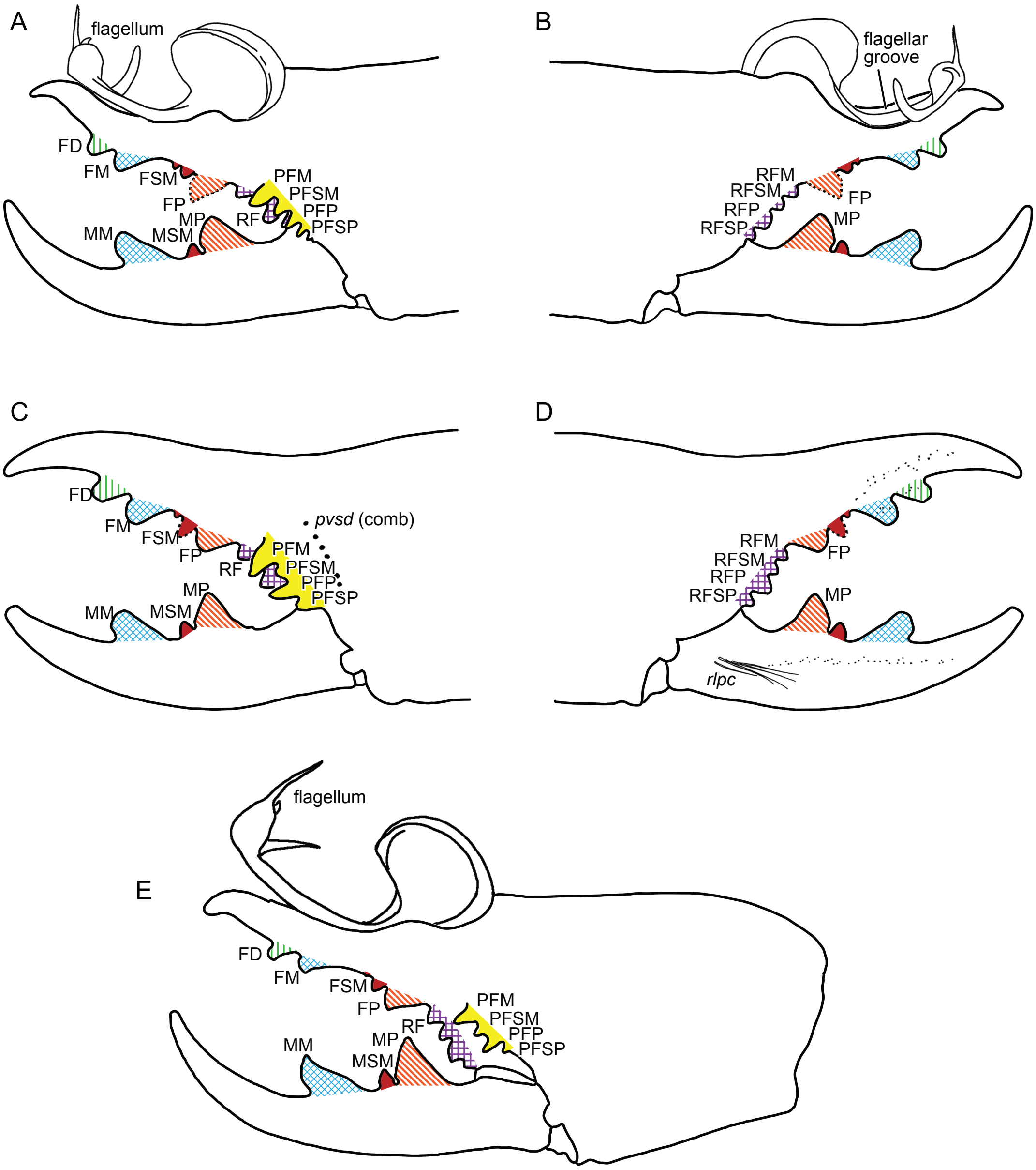

A
flagellum
FD
FM
FSM
FP
MP
MM
MSM
RF
PFM
PFSM
PFP
PFSP
B
flagellar groove
RFM
RFSM
RFP
RFSP
FP
MP
C
FD
FM
FSM
FP
RF
pvsd (comb)
PFM
PFSM
PFP
PFSP
MP
MM
MSM
D
RFM
RFSM
RFP
RFSP
FP
MP
rlpc
E
flagellum
FD
FM
FSM
FP
PFM
PFSM
PFP
PFSP
RF
MP
MM
MSM

PLATE 114. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A–D.** *Solpuguna* cf. *orangica*. **A, B.** ♂ (AMNH [LP 5969]). **C, D.** ♀ (AMNH [LP 5969]). **E.** *Solpuguna alcicornis* (Kraepelin, 1914), syntype ♂ (ZMUH [R8515]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (sockets of setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

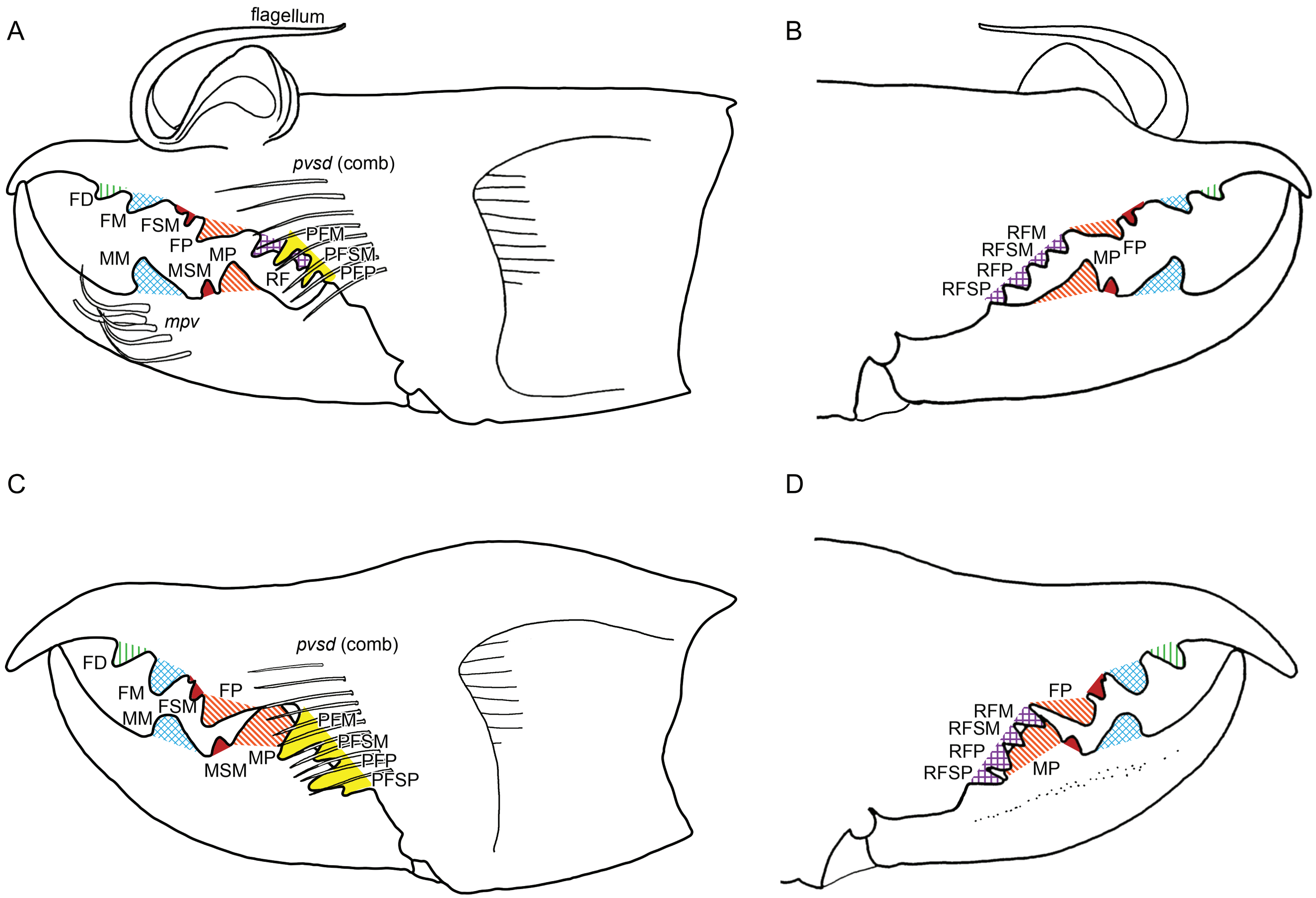

A
flagellum
pvsd (comb)
FD
FM
FSM
FP
MM
MSM
MP
PFM
PFSM
PFP
RF
mpv
B
RFM
RFSM
RFP
RFSP
MP
FP
C
pvsd (comb)
FD
FM
MM
FSM
FP
MSM
MP
PFM
PFSM
PFP
PFSP
D
FP
RFM
RFSM
RFP
RFSP
MP

PLATE 115. Solpugidae Leach, 1815, *Solpugyla* sp., chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 10764]). **C, D.** ♀ (AMNH [LP 10764]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***mpv*,** movable finger, proventral setae (four apicalmost *mpv* setae illustrated in **A**); **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

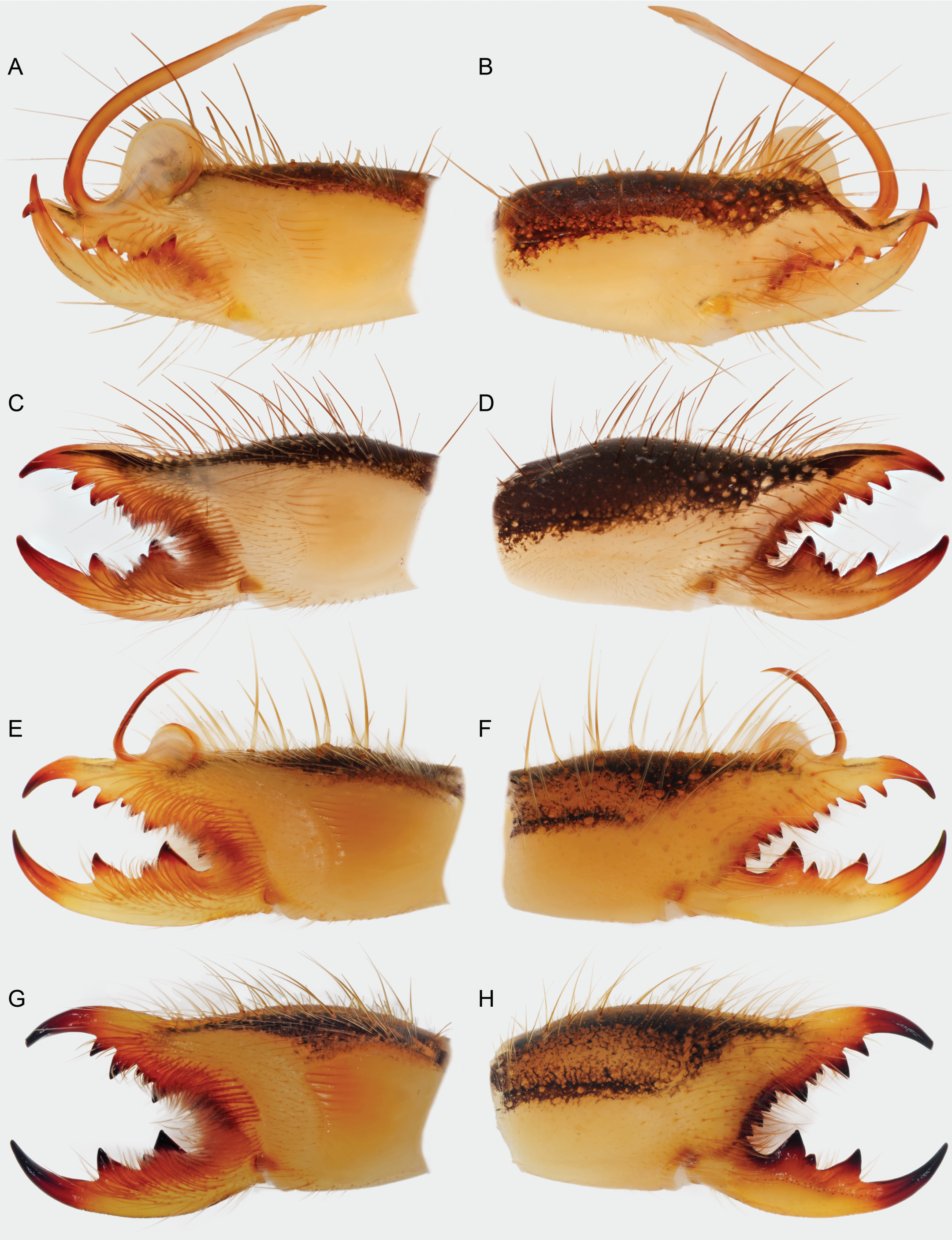


PLATE 116. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A–D.** *Zeria fusca* (C.L. Koch, 1842). **A, B.** ♂ (AMNH [LP 1473]). **C, D.** ♀ (AMNH [LP 1472]). **E–H.** *Zeria sericea* (Pocock, 1897). **E, F.** ♂ (NMNW 13801). **G, H.** ♀ (NMNW 13801).

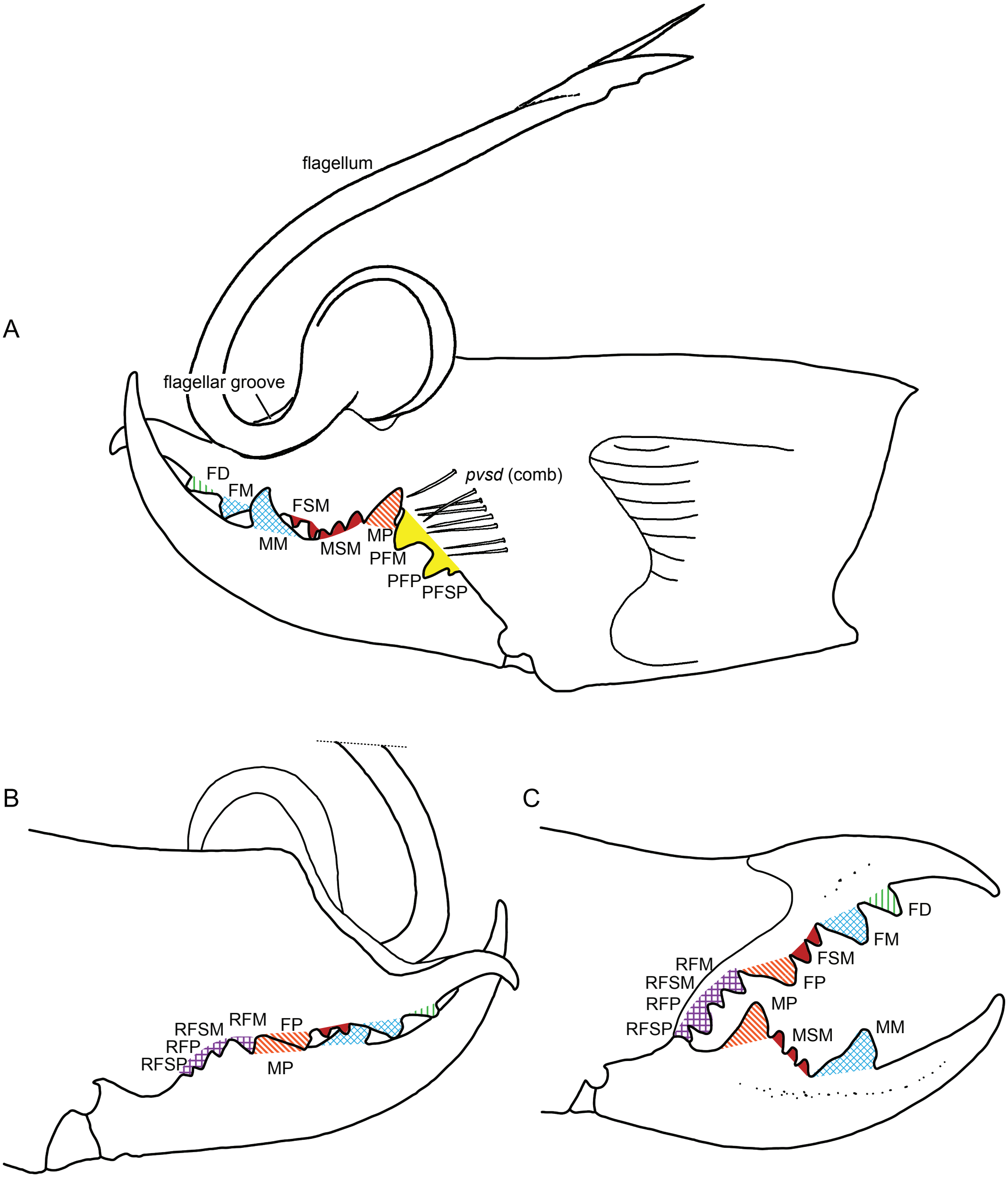

A
flagellum
flagellar groove
FD
FM
FSM
MM
MSM
MP
PFM
PFP
PFSP
pvsd (comb)
B
RFSM
RFM
FP
RFP
RFSP
MP
C
FD
FM
FSM
FP
RFM
RFSM
RFP
RFSP
MP
MSM
MM

PLATE 117. Solpugidae Leach, 1815, *Zeria fusca* (C.L. Koch, 1842), chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 1473]). **C.** ♀ (AMNH [LP 1472]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

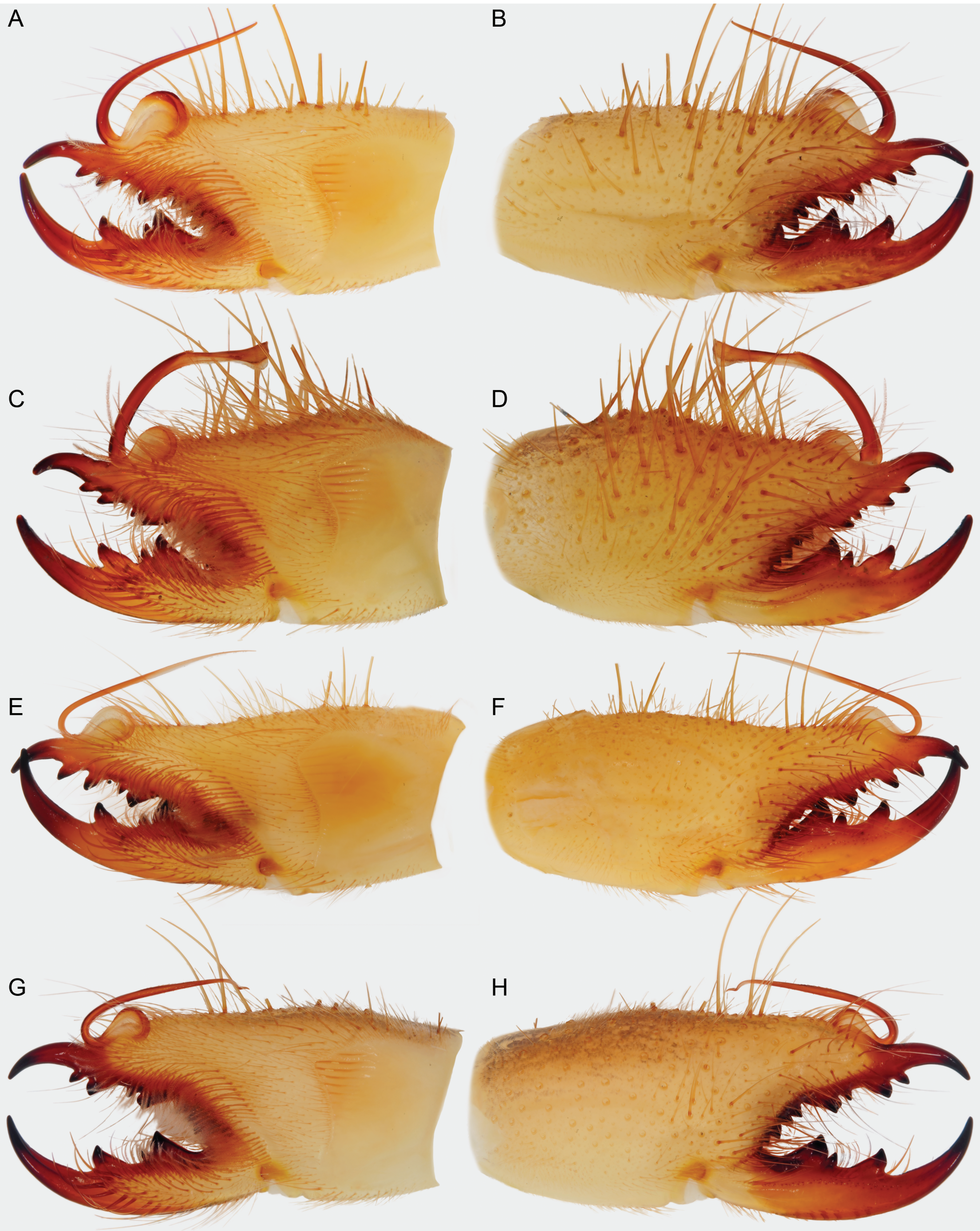


PLATE 118. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Zeria adunca* (Roewer, 1933), ♂ (MRAC 216.105). **C, D.** *Zeria fordi* (Hirst, 1907), ♂ (AMNH [LP 9090]). **E, F.** *Zeria glabricornis* (Lawrence, 1928), ♂ (AMNH [LP 3614]). **G, H.** *Zeria keyserlingi* (Pocock, 1895), ♂ (AMNH [LP 4632]).

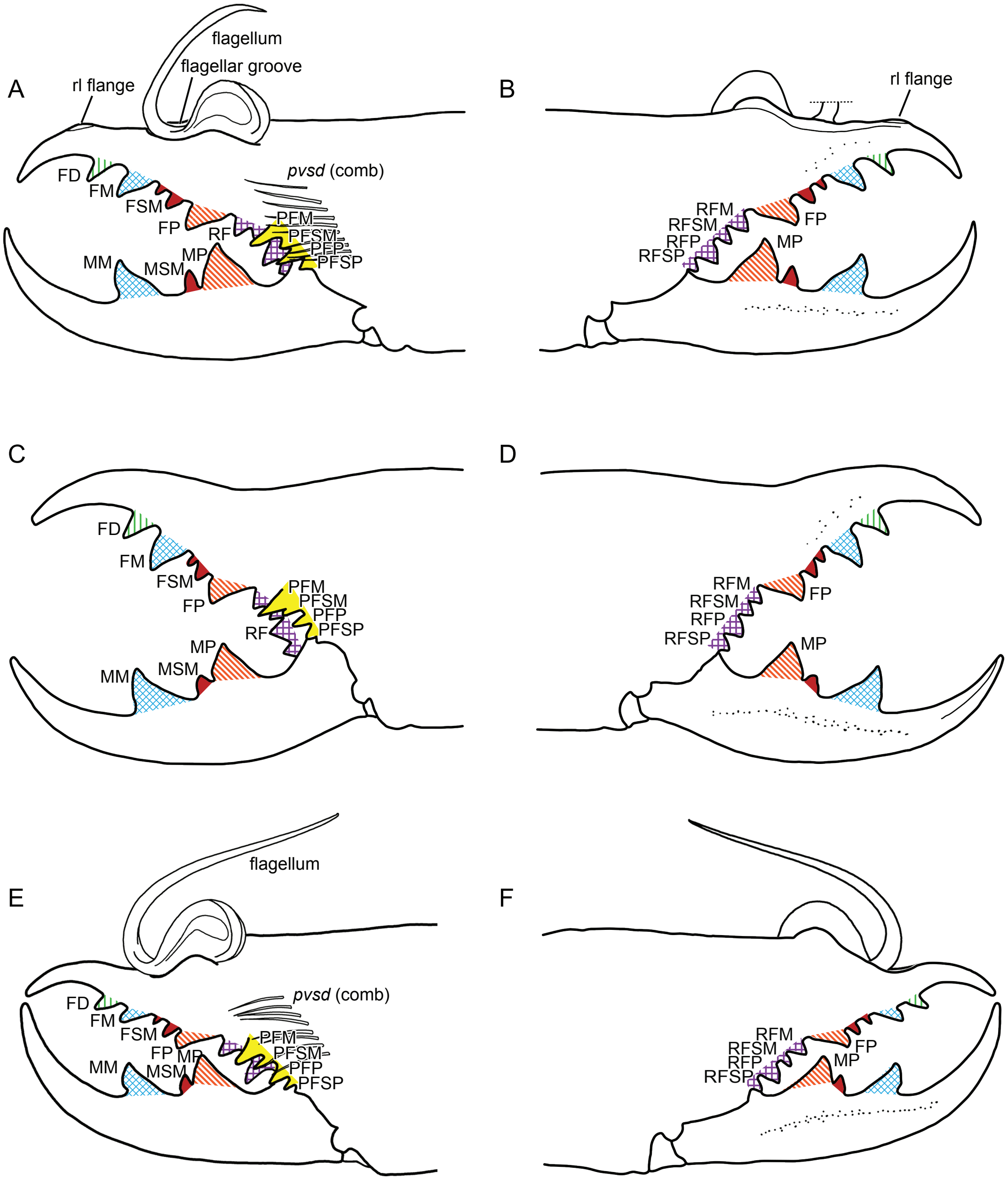

A
rl flange
flagellum
flagellar groove
pvsd (comb)
FD
FM
FSM
FP
RF
PFM
PFSM
PFP
PFSP
MM
MSM
MP
B
rl flange
RFM
RFSM
RFP
RFSP
FP
MP
C
FD
FM
FSM
FP
PFM
PFSM
PFP
PFSP
RF
MP
MM
MSM
D
RFM
RFSM
RFP
RFSP
FP
MP
E
flagellum
pvsd (comb)
FD
FM
FSM
FP
MP
MM
MSM
PFM
PFSM
PFP
PFSP
F
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 119. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D, F**) views, illustrating dentition, setae, and flagellum. **A–D.** *Zeria sericea* (Pocock, 1897). **A, B.** ♂ (NMNW 13801). **C, D.** ♀ (NMNW 13801). **E, F.** *Zeria adunca* (Roewer, 1933), ♂ (MRAC 216.105). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; **rl,** retrolateral.

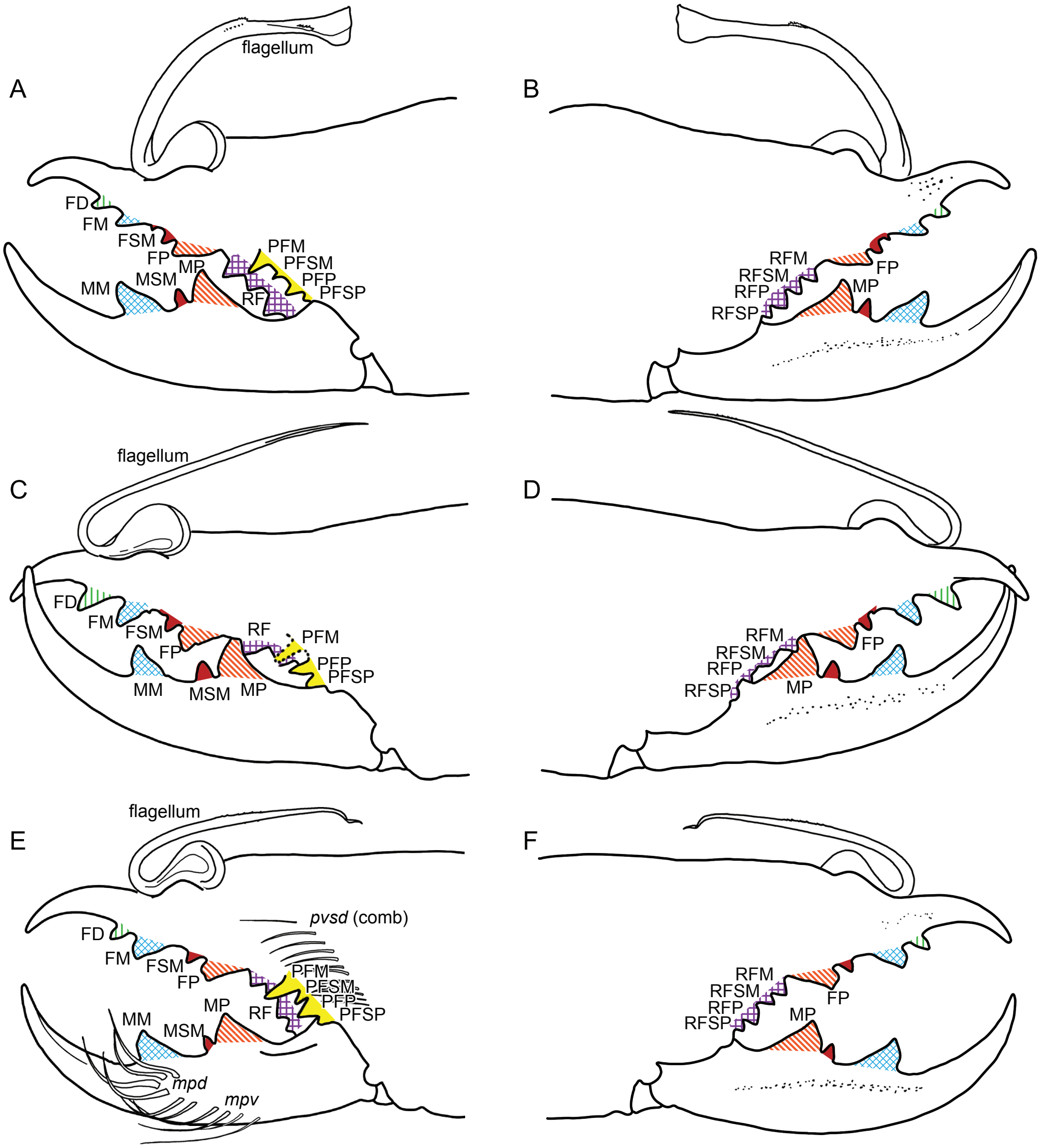

A
flagellum
FD
FM
FSM
FP
MP
MSM
MM
PFM
PFSM
PFP
PFSP
RF
B
RFM
RFSM
RFP
RFSP
FP
MP
C
flagellum
FD
FM
FSM
FP
MM
MSM
MP
RF
PFM
PFP
PFSP
D
RFM
RFSM
RFP
RFSP
FP
MP
E
flagellum
pvsd (comb)
FD
FM
FSM
FP
MP
MM
MSM
RF
PFM
PFSM
PFP
PFSP
mpd
mpv
F
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 120. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D, F**) views, illustrating dentition, setae, and flagellum. **A, B.** *Zeria fordi* (Hirst, 1907), ♂ (AMNH [LP 9090]). **C, D.** *Zeria glabricornis* (Lawrence, 1928), ♂ (AMNH [LP 3614]). **E, F.** *Zeria keyserlingi* (Pocock, 1895), ♂ (AMNH [LP 4632]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***mpd*,** movable finger, proventral setae (only distalmost two indicated); ***mpv*,** movable finger, proventral setae (not all setae indicated); **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

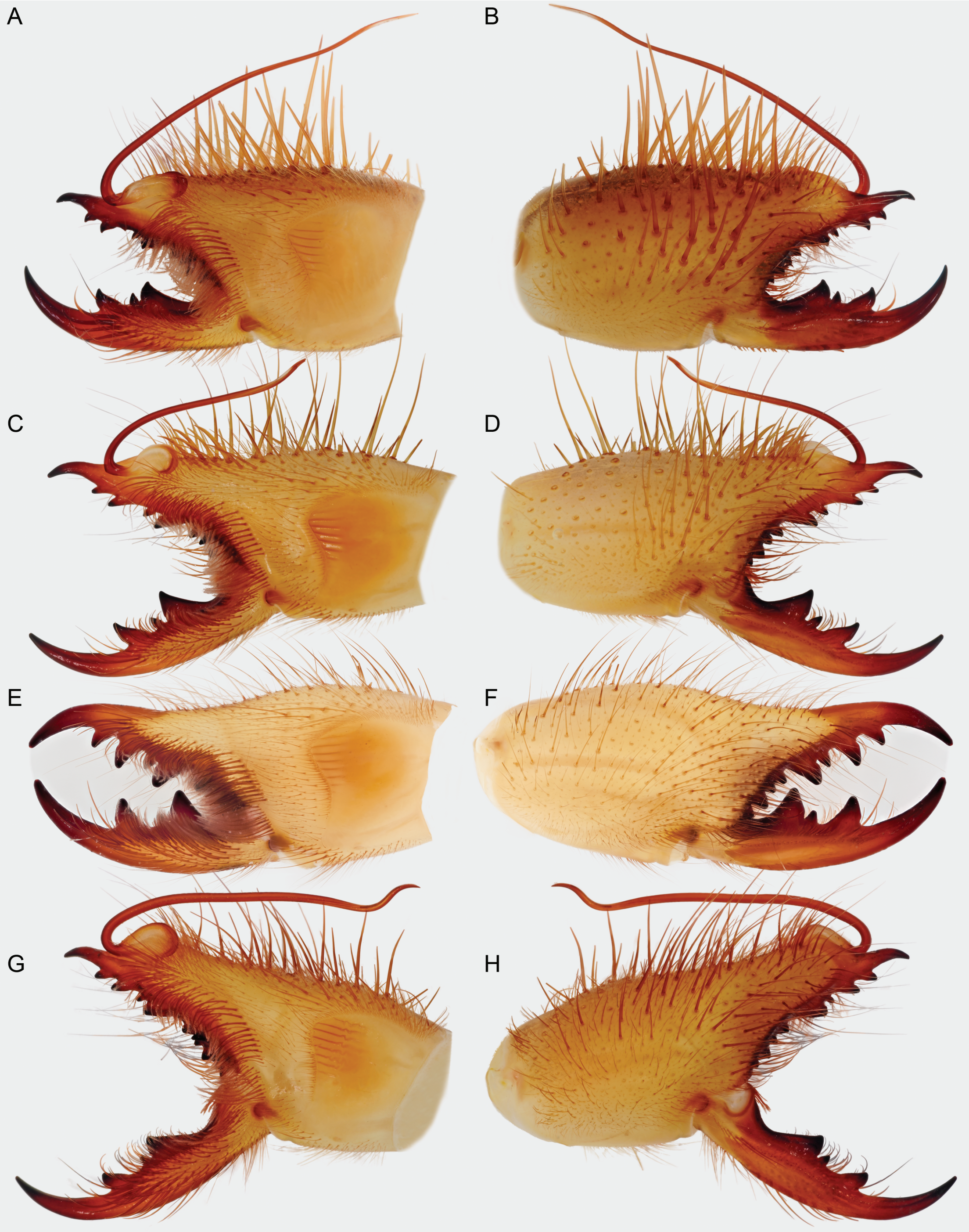
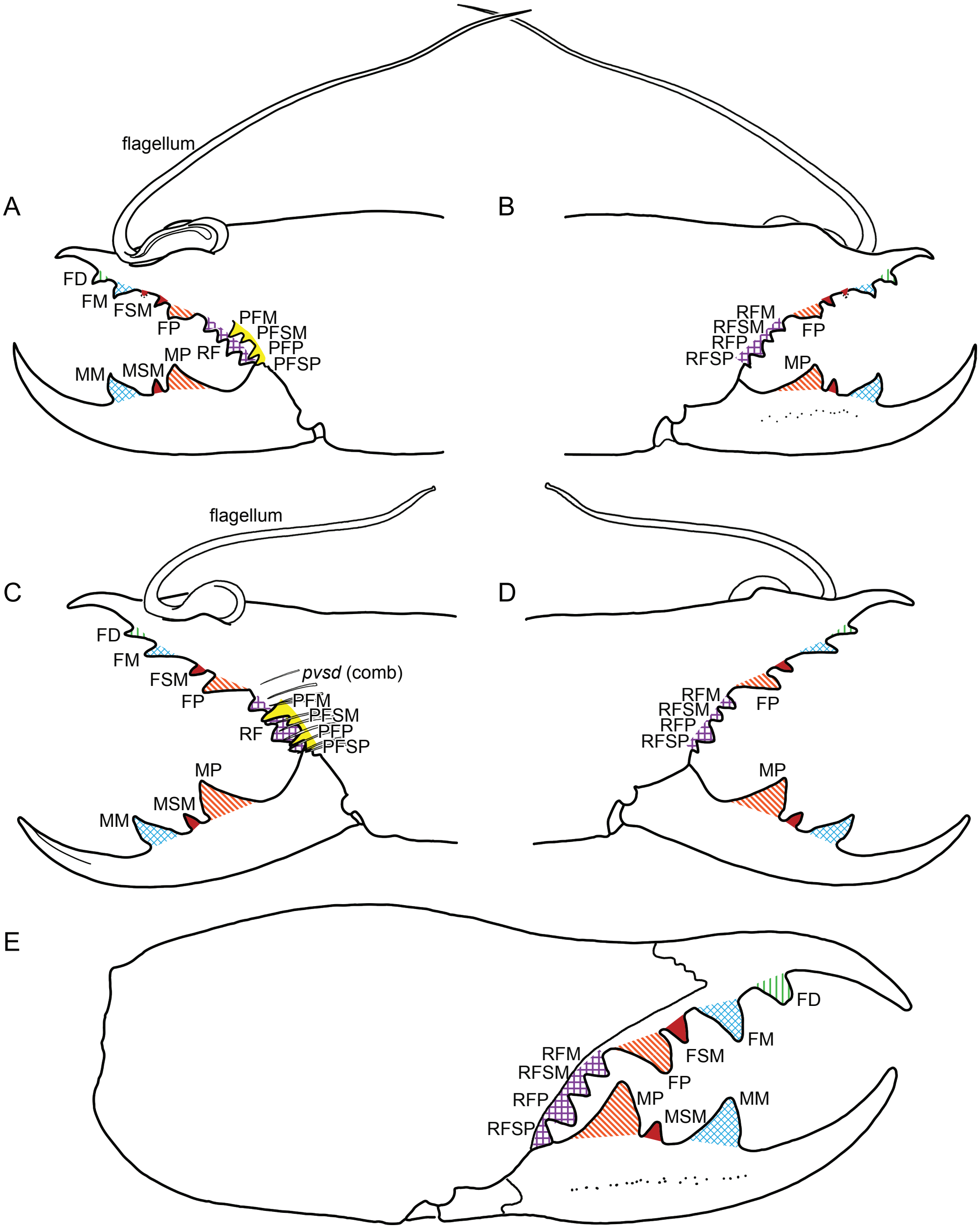


PLATE 121. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **C–F.** *Zeria lawrencei* (Roewer, 1933). **C, D.** ♂ (AMNH [LP 9906]). **E, F.** ♀ (NMNW 13820). **G, H.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]).


flagellum
A
FD
FM
FSM
FP
PFM
PFSM
PFP
PFSP
MP
RF
MM
MSM
B
RFM
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RFP
RFSP
FP
MP
flagellum
C
FD
FM
FSM
FP
pvsd (comb)
PFM
PFSM
PFP
PFSP
RF
MP
MSM
MM
D
RFM
RFSM
RFP
RFSP
FP
MP
E
FD
FM
RFM
RFSM
FSM
FP
RFP
MP
MSM
MM
RFSP

PLATE 122. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C**) and retrolateral (**B, D, E**) views, illustrating dentition, setae, and flagellum. **A, B.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **C–E.** *Zeria lawrencei* (Roewer, 1933). **C, D.** ♂ (AMNH [LP 9906]). **E.** ♀ (NMNW 13820). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

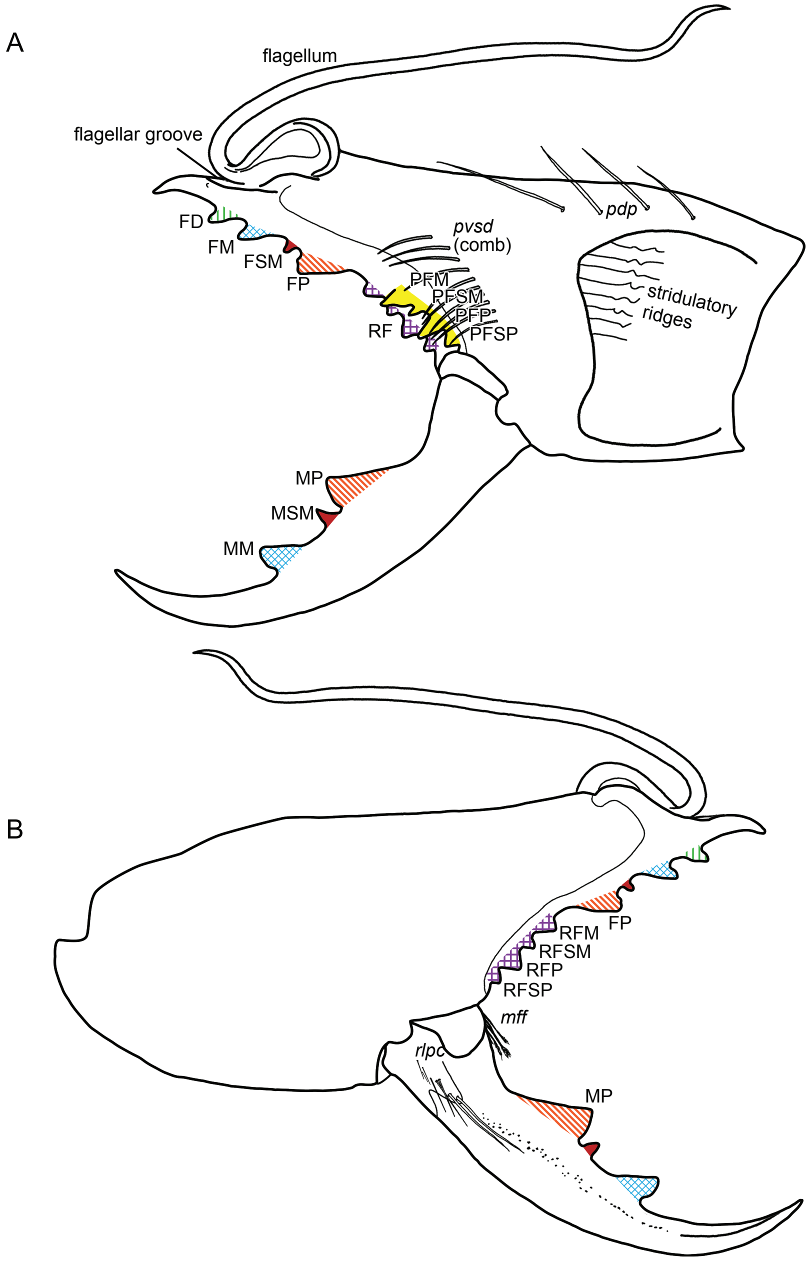

A
flagellum
flagellar groove
FD
FM
FSM
FP
pvsd
(comb)
pdp
PFM
PFSM
PFP
PFSP
RF
stridulatory
ridges
MP
MSM
MM
B
FP
RFM
RFSM
RFP
RFSP
mff
rlpc
MP

PLATE 123. Solpugidae Leach, 1815, *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]), chelicerae, prolateral (**A**) and retrolateral (**B**) views, illustrating dentition, setae, and flagellum. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; ***mff*,** movable finger, fondal setae; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

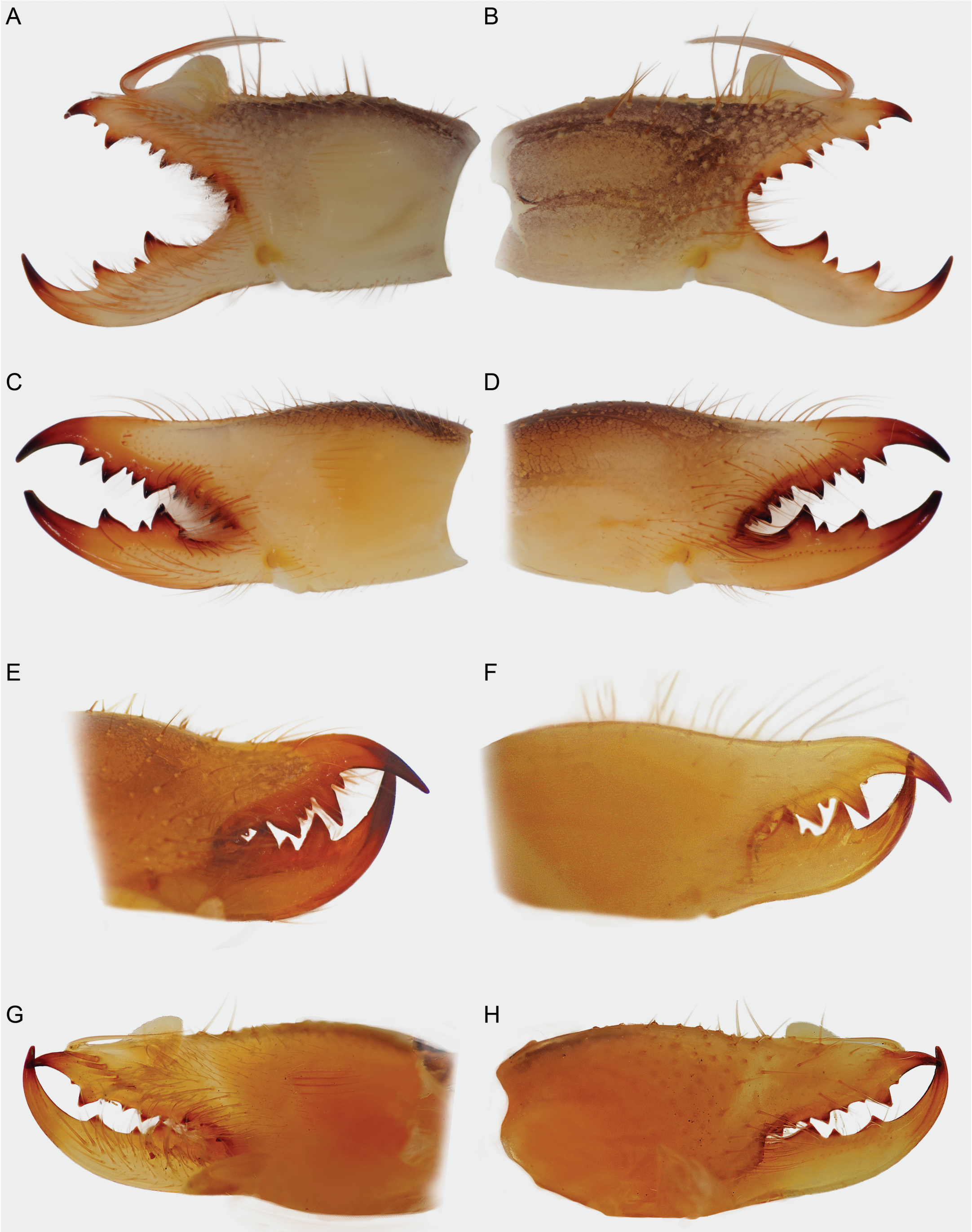


PLATE 124. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, G**) and retrolateral (**B, D–F, H**) views. **A–D.** *Zeriassa furcicornis* Lawrence, 1929. **A, B.** ♂ (AMNH [LP 3612]). **C, D.** ♀ (AMNH [LP 9848]). **E.** *Zeriassa* sp., ♀ (MCZ 126318). **F.** *Zeriassa* sp., 3-claw stage juv. (MCZ 126318). **G, H.** *Solpugisticella kenyae* Turk, 1960, holotype ♂ (HUJI).

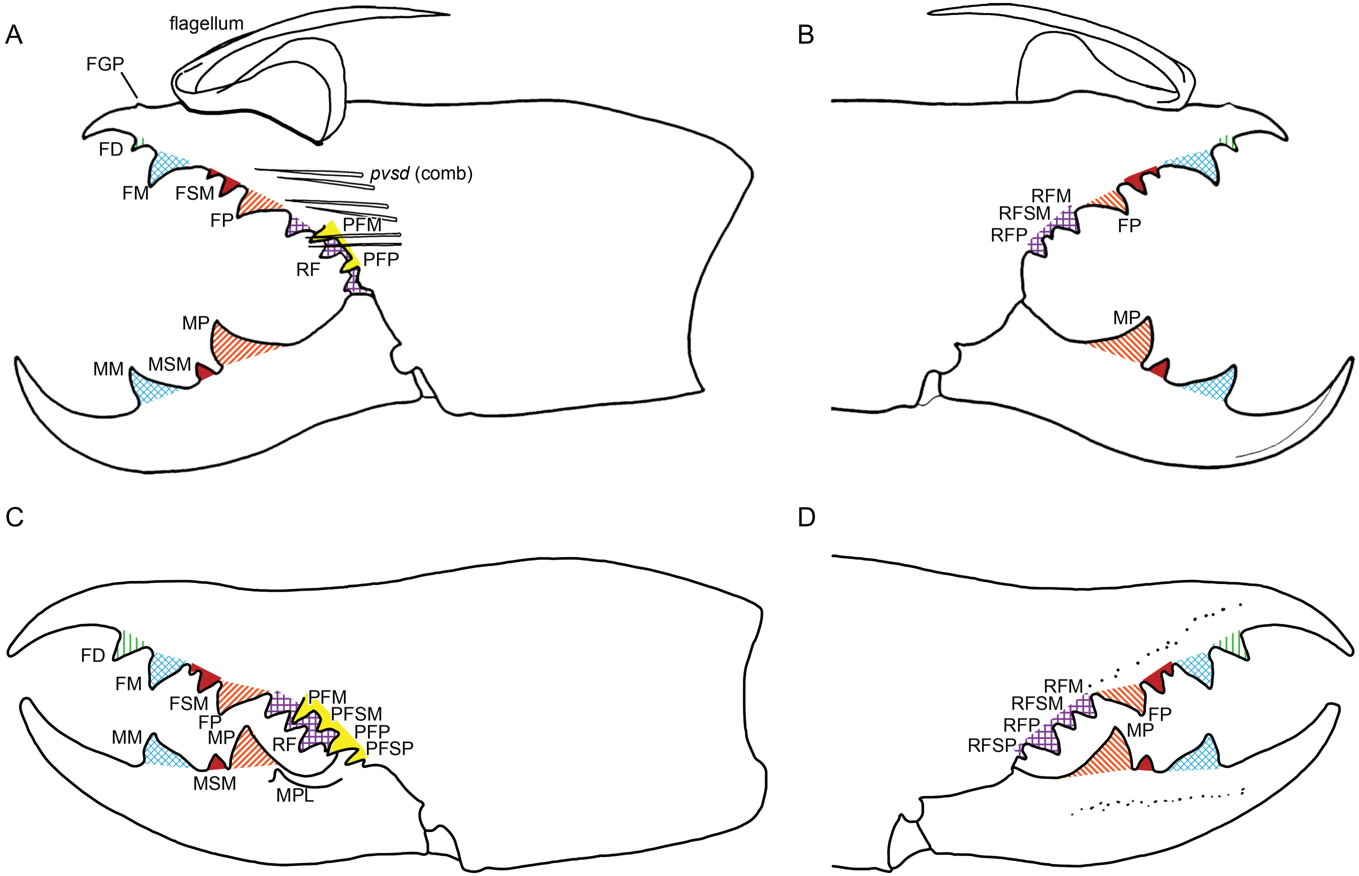

A
flagellum
FGP
FD
FM
FSM
FP
pvsd (comb)
PFM
PFP
RF
MP
MM
MSM
B
RFM
RFSM
RFP
FP
MP
C
FD
FM
FSM
FP
MP
MM
PFM
PFSM
PFP
PFSP
RF
MSM
MPL
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 125. Solpugidae Leach, 1815, *Zeriassa furcicornis* Lawrence, 1929, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 3612]). **C, D.** ♀ (AMNH [LP 9848]). Abbreviations: **FD,** fixed finger, distal tooth; **FGP,** flagellar groove process; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

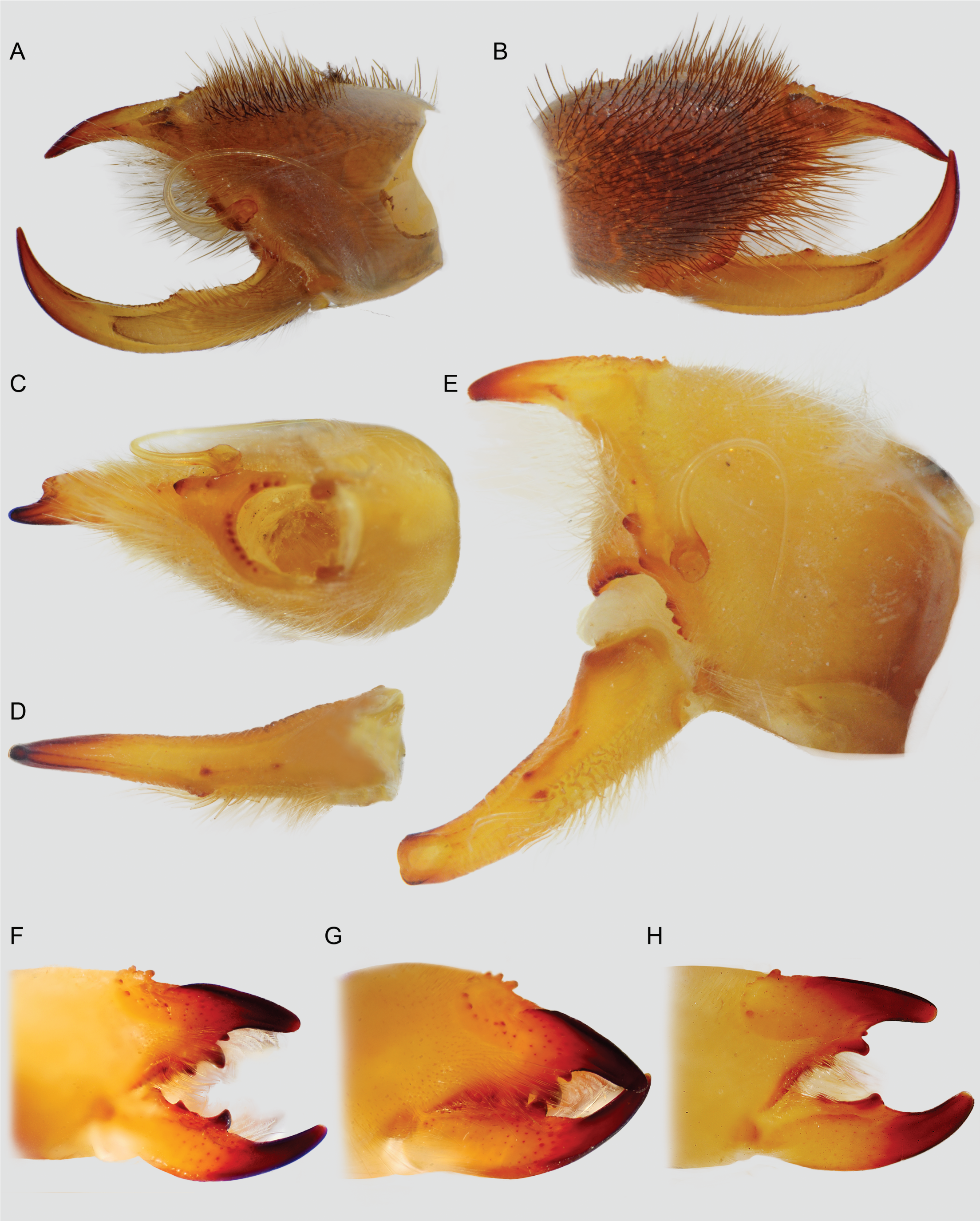


PLATE 126. Hexisopodidae Pocock, 1897, chelicerae, prolateral (**A**), retrolateral (**B, F–H**) and proventral (**E**) views, paturon, ventral view (**C**), and movable finger, dorsal view (**D**). **A, B.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426). **C–E.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795). **F, G.** *Hexisopus* sp., juv. (NMNW 11098). **H.** *Hexisopus aureopilosus* Lawrence, 1968, ♀ (NMNW 11203).

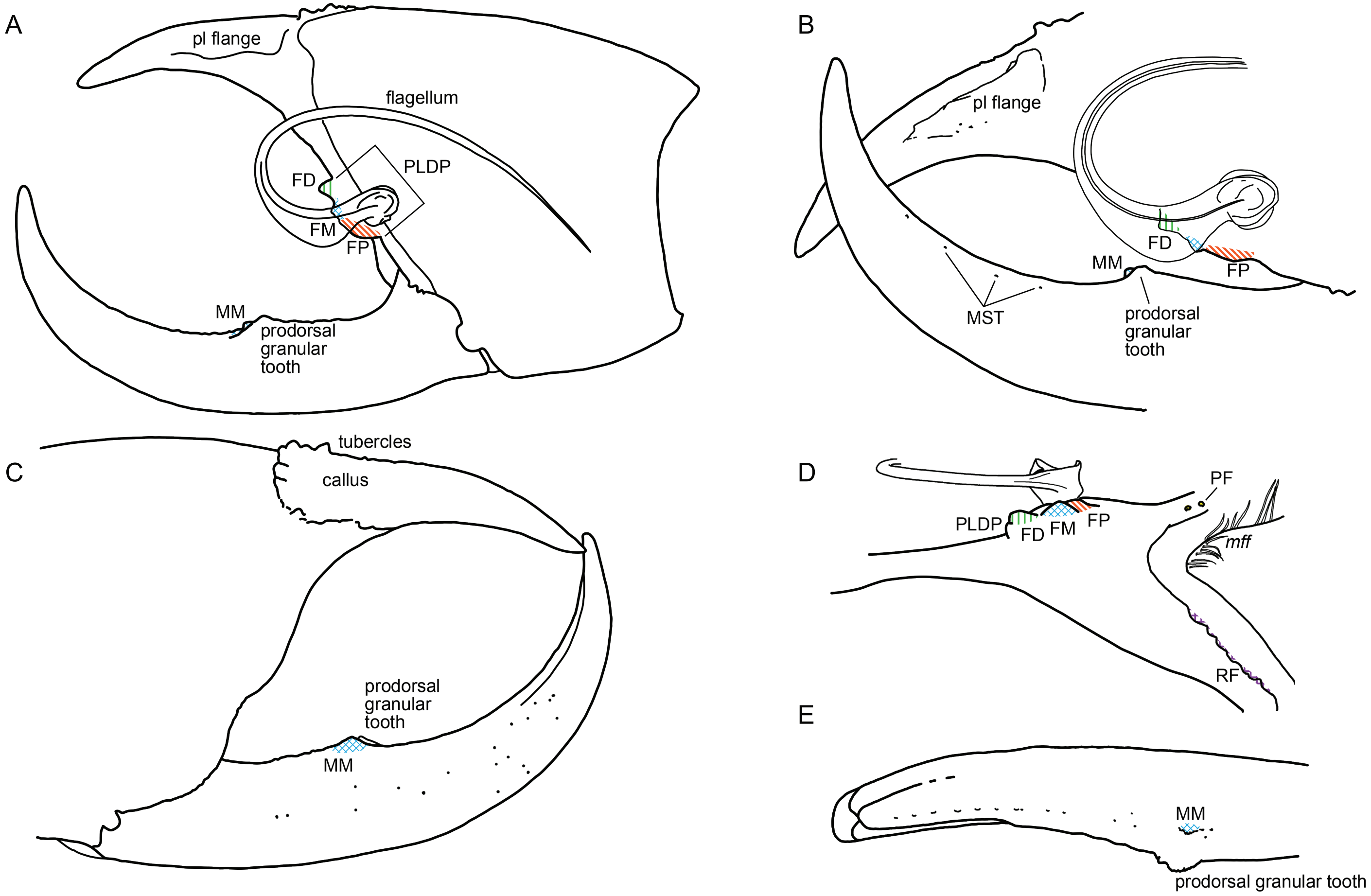

A
pl flange
flagellum
PLDP
FD
FM
FP
MM
prodorsal granular tooth
B
pl flange
FD
MM
FP
MST
prodorsal granular tooth
C
tubercles
callus
prodorsal granular tooth
MM
D
PF
PLDP
FD
FM
FP
mff
RF
E
MM
prodorsal granular tooth

PLATE 127. Hexisopodidae Pocock, 1897, *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426), chelicerae, prolateral (**A, B**) and retrolateral (**C**) views, fixed finger fondal area, ventral view (**D**), and movable finger, dorsal view (**E**), illustrating dentition, setae, and flagellum. PLDP hypothesized to be fused with primary teeth. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; ***mff*,** movable finger, fondal setae; **MM,** movable finger, medial tooth; **MST,** movable finger, subterminal teeth (denticlelike serrations on gnathal edge of finger); **PF,** profondal teeth; **pl,** prolateral; **PLDP,** prolateral dental process; **RF,** retrofondal teeth.

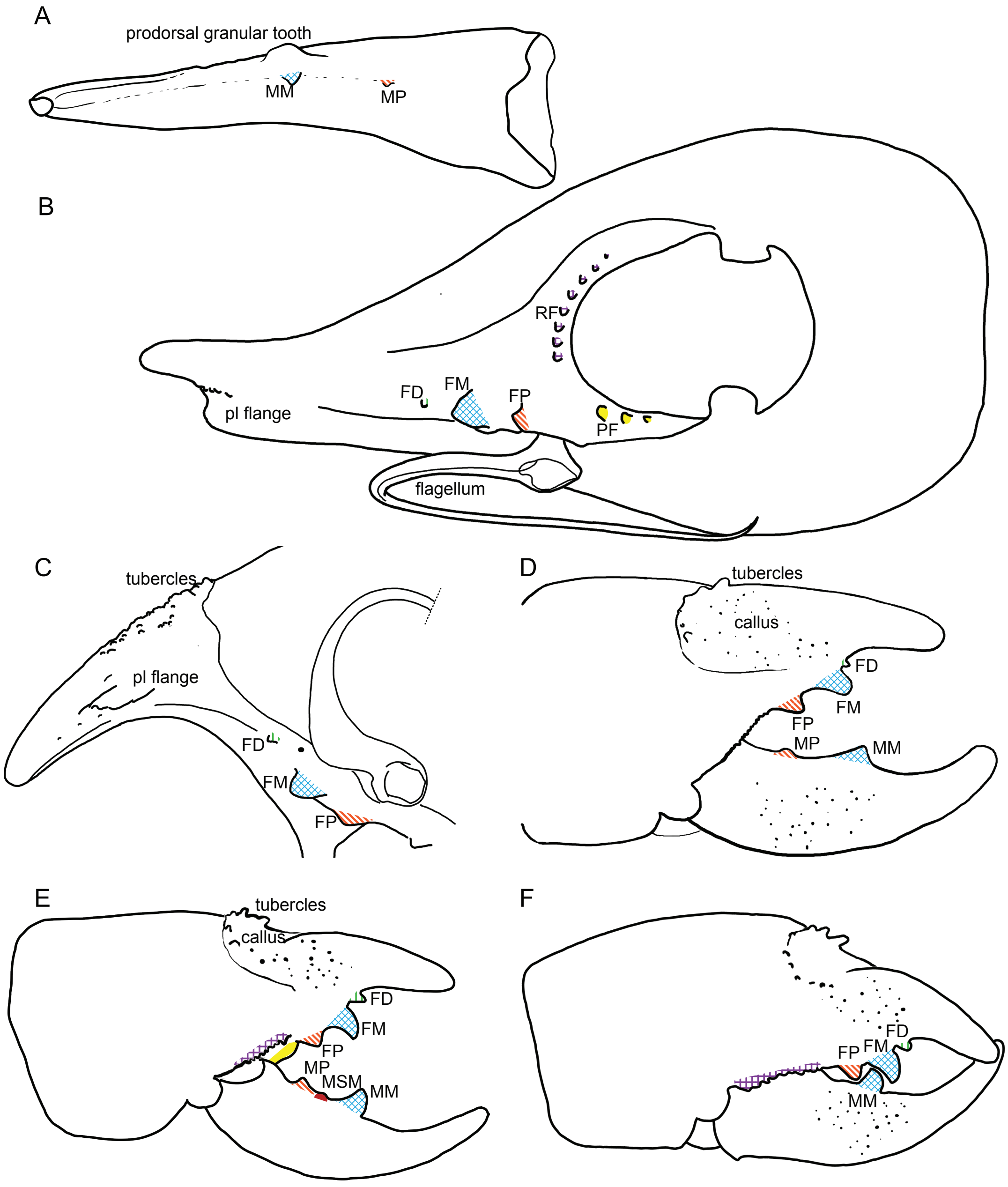

A
prodorsal granular tooth
MM
MP
B
RF
FD
FM
FP
PF
pl flange
flagellum
C
tubercles
pl flange
FD
FM
FP
D
tubercles
callus
FD
FM
FP
MP
MM
E
tubercles
callus
FD
FM
FP
MP
MSM
MM
F
FD
FP
FM
MM

PLATE 128. Hexisopodidae Pocock, 1897, cheliceral movable finger, dorsal view (**A**), paturon, ventral view (**B**), fixed finger, prolateral view (**C**), and chelicerae, retrolateral views (**D–F**), illustrating dentition, setae, and flagellum. **A–C.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795). **D.** *Hexisopus* sp., juv. (NMNW 11098). **E, F.** *Hexisopus aureopilosus* Lawrence, 1968, ♀ (NMNW 11203). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger submedial tooth; **PF,** profondal teeth; **pl,** prolateral; **RF,** retrofondal teeth.

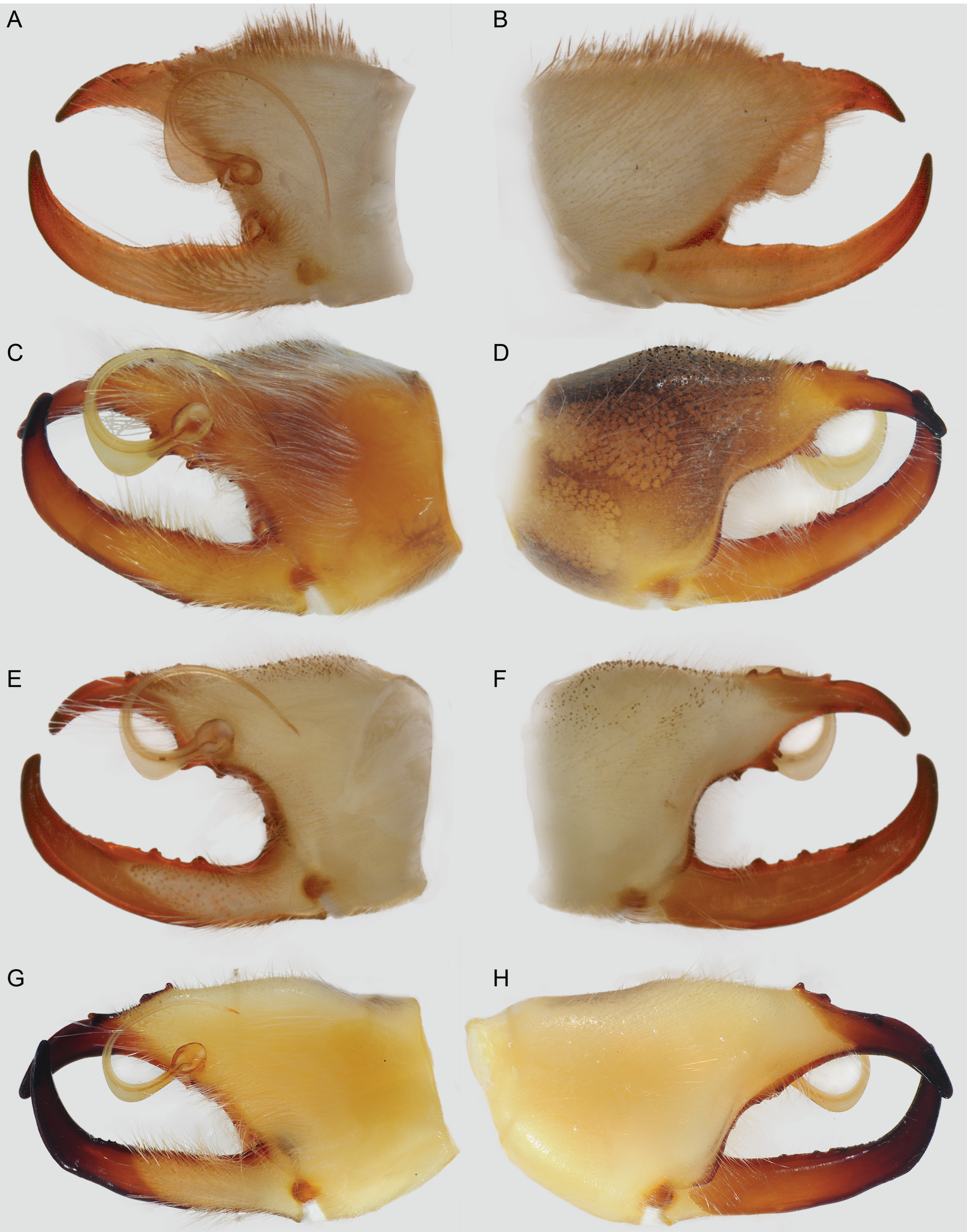


PLATE 129. Hexisopodidae Pocock, 1897, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Hexisopus psammophilus* Wharton, 1981, ♂ (AMNH [LP 9858]). **C–F.** *Chelypus hirsti* Hewitt, 1915. **C, D.** ♂ (NMNW 10804). **E, F.** ♂ (NMNW 11202). **G, H.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632).

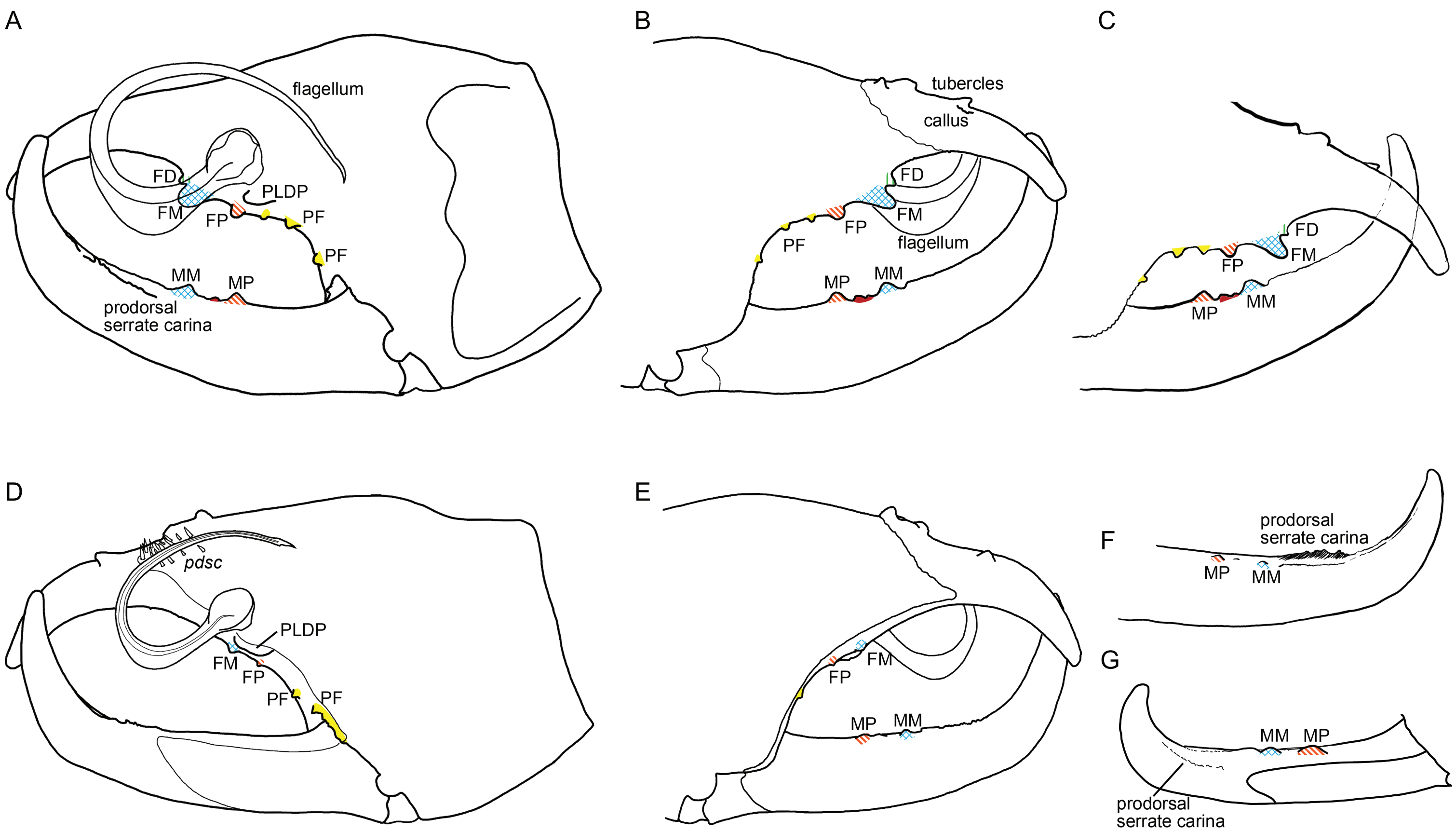

A
flagellum
FD
PLDP
FM
FP
PF
PF
MM
MP
prodorsal serrate carina
B
tubercles
callus
FD
FP
FM
PF
flagellum
MP
MM
C
FD
FM
FP
MP
MM
D
pdsc
PLDP
FM
FP
PF
PF
E
FM
FP
MP
MM
F
prodorsal serrate carina
MP
MM
G
MM
MP
prodorsal serrate carina

PLATE 130. Hexisopodidae Pocock, 1897, chelicerae, prolateral (**A, D**) and retrolateral views (**B, C, E**), and movable finger, retrodorsal (**F**) and prodorsal (**G**) views. **A–C, F.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **D, E, G.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***pdsc*,** prodorsal spiniform setal cluster; **PF,** profondal teeth; **PLDP,** prolateral dental process.

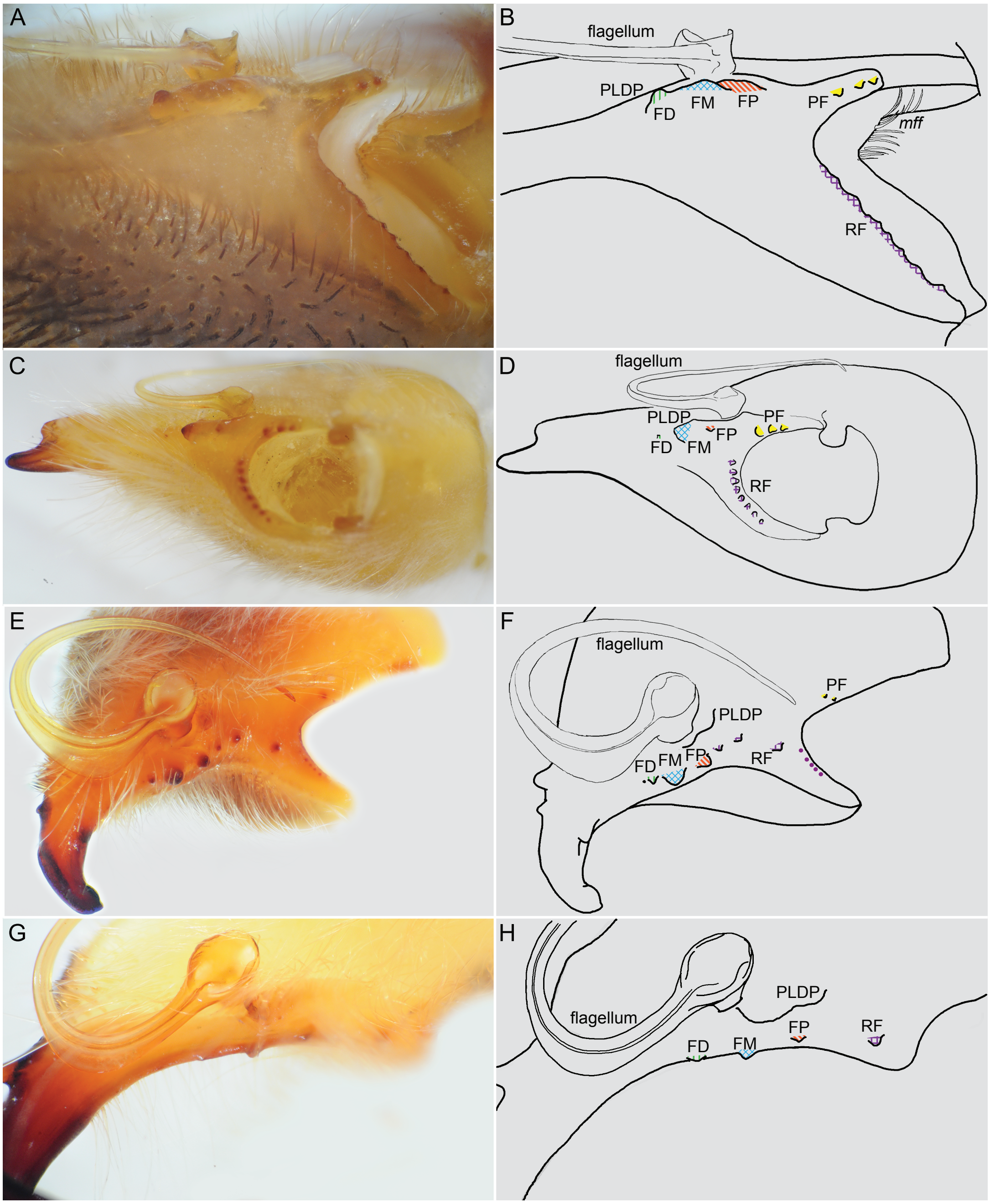

A
B
flagellum
PLDP
FD
FM
FP
PF
mff
RF
C
D
flagellum
PLDP
PF
FD
FM
FP
RF
E
F
flagellum
PF
PLDP
FD
FM
FP
RF
G
H
flagellum
PLDP
FP
RF
FD
FM

PLATE 131. Hexisopodidae Pocock, 1897, cheliceral fixed fingers (**A, B, E–H**) and paturon (**C, D**), ventral (**A–D**) and proventral (**E–H**) views illustrating fondal area. **A, B.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426). **C, D.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795). **E, F.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **G, H.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; ***mff*,** movable finger, fondal setae; **PLDP,** prolateral dental process; **PF,** profondal teeth; **RF,** retrofondal teeth.

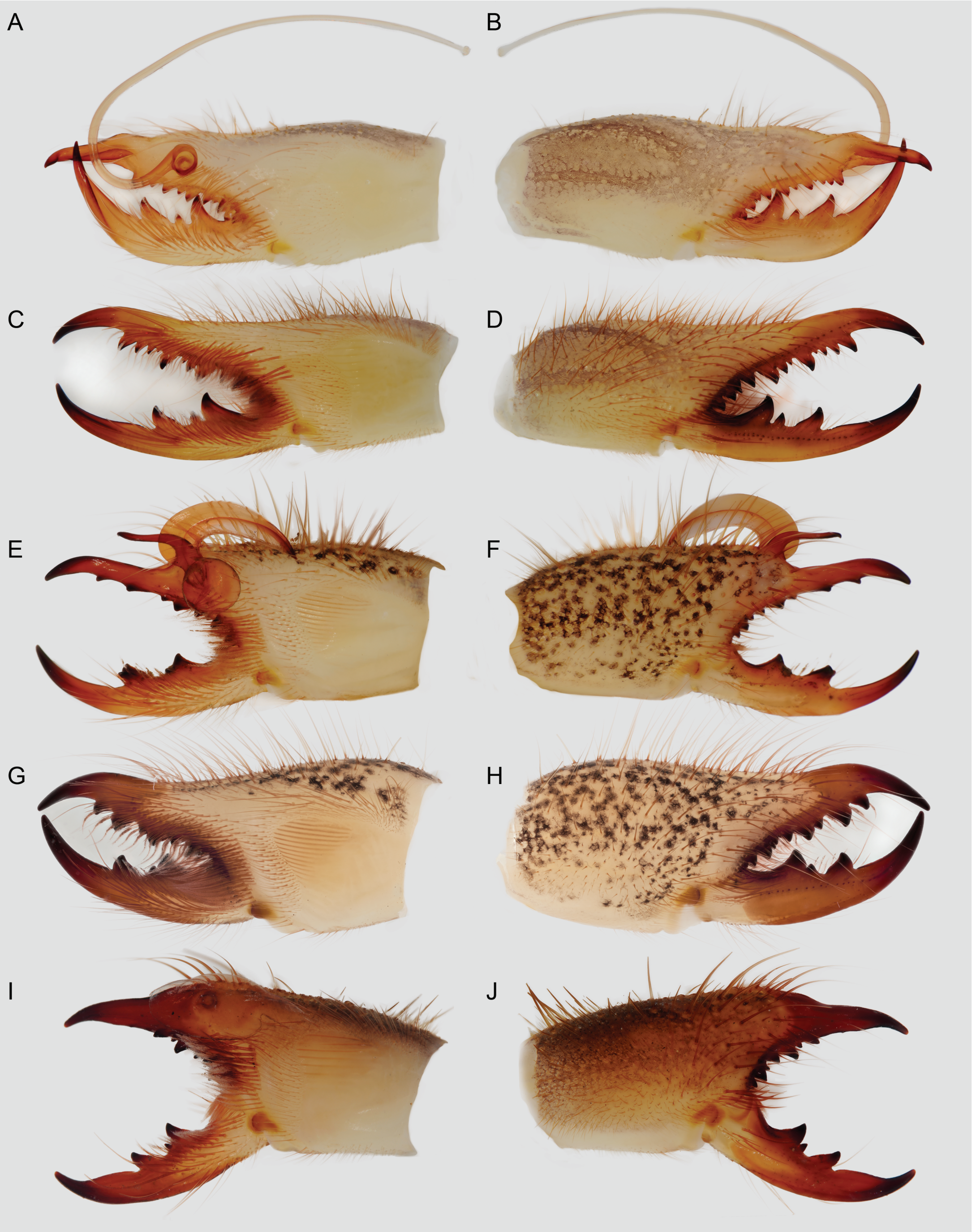


PLATE 132. Daesiidae Kraepelin, 1899 (**A–J**), including Namibesiinae Wharton, 1981 (**A–D**), chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Namibesia pallida* Lawrence, 1962. **A, B.** ♂ (AMNH [LP 10721]). **C, D.** ♀ (AMNH [LP 4017]). **E–H.** *Ammotrechelis goetschi* Roewer, 1934. **E, F.** ♂ (AMNH [LP 10673]). **G, H.** ♀ (AMNH [LP 10673]). **I, J.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]).

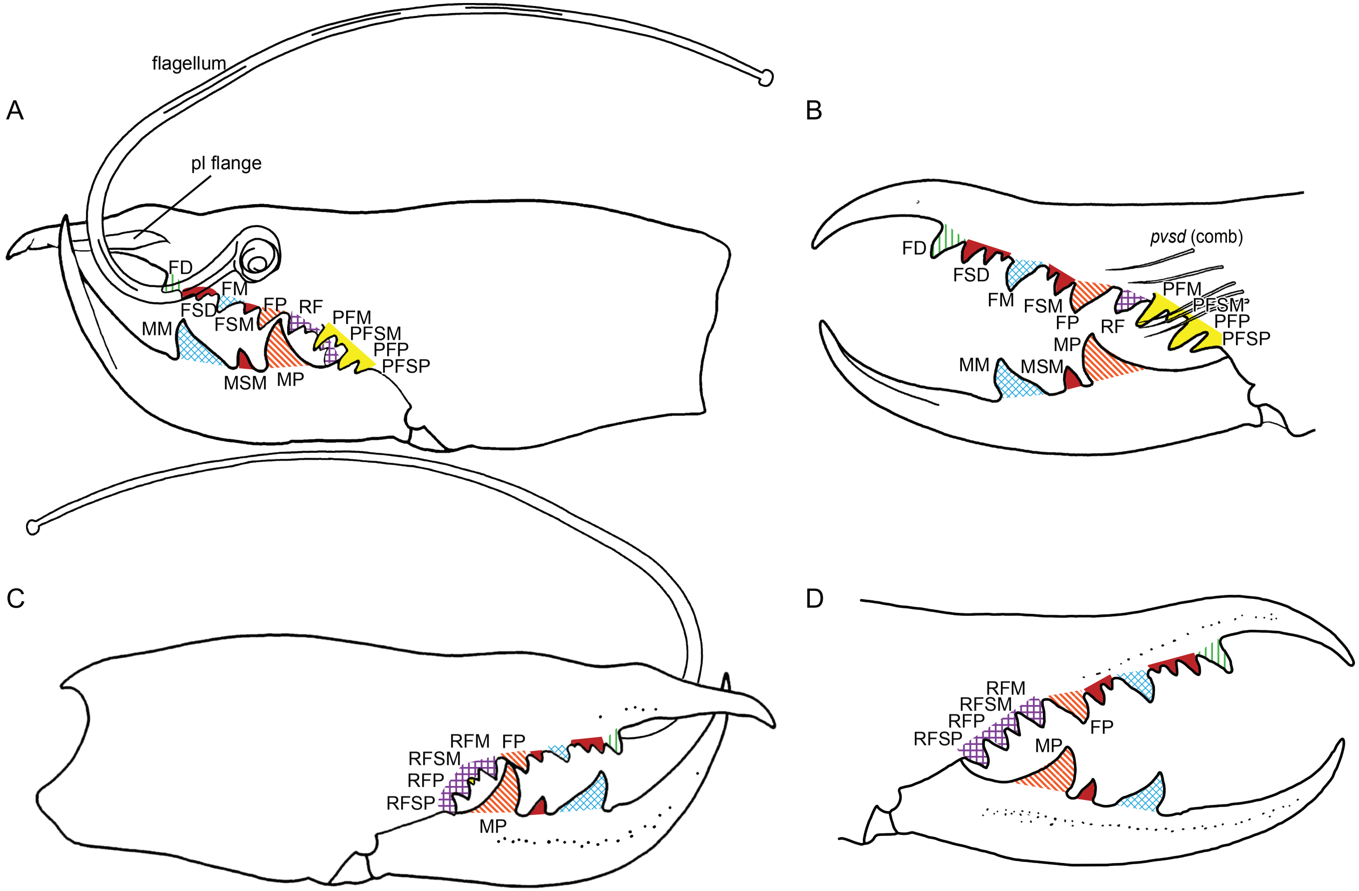

A
flagellum
pl flange
FD
FM
FSD
FSM
FP
RF
PFM
PFSM
PFP
PFSP
MM
MSM
MP
B
pvsd (comb)
FD
FSD
FM
FSM
FP
RF
PFM
PFSM
PFP
PFSP
MP
MM
MSM
C
RFM
FP
RFSM
RFP
RFSP
MP
D
RFM
RFSM
RFP
RFSP
FP
MP

PLATE 133. Daesiidae Kraepelin, 1899, Namibesiinae Wharton, 1981, *Namibesia pallida* Lawrence, 1962, chelicerae, prolateral (**A, B**) and retrolateral (**C, D**) views illustrating dentition, setae, and flagellum. **A, C.** ♂ (AMNH [LP 10721]). **B, D.** ♀ (AMNH [LP 4017]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **pl,** prolateral; ***pvsd,*** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

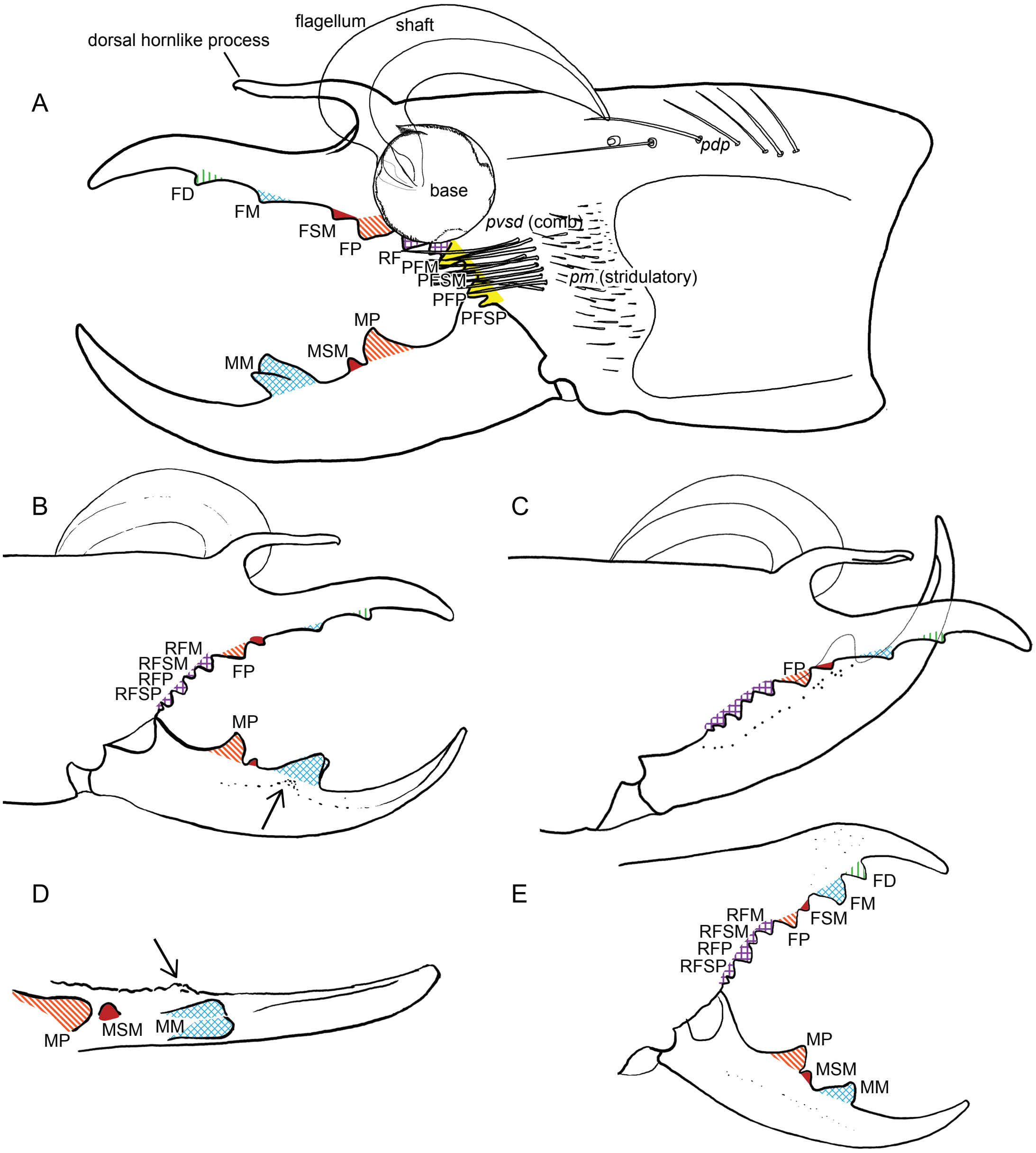

A
flagellum
shaft
dorsal hornlike process
base
pdp
FD
FM
FSM
FP
RF
PFM
PFSM
PFP
PFSP
pvsd (comb)
pm (stridulatory)
MP
MSM
MM
B
RFM
RFSM
RFP
RFSP
FP
MP
C
FP
D
MP
MSM
MM
E
FD
FM
FSM
FP
RFM
RFSM
RFP
RFSP
MP
MSM
MM

PLATE 134. Daesiidae Kraepelin, 1899, *Ammotrechelis goetschi* Roewer, 1934, chelicerae, prolateral (**A**) and retrolateral (**B, C, E**) views, and movable finger, dorsal view (**D**), illustrating dentition, setae, and flagellum. **A–D.** ♂ (AMNH [LP 10673]). **E.** ♀ (AMNH [LP 10673]). Arrows indicate blunt retrolateral granular tubercle. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pdp*,** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pm*,** promedial setae (stridulatory setae only); ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

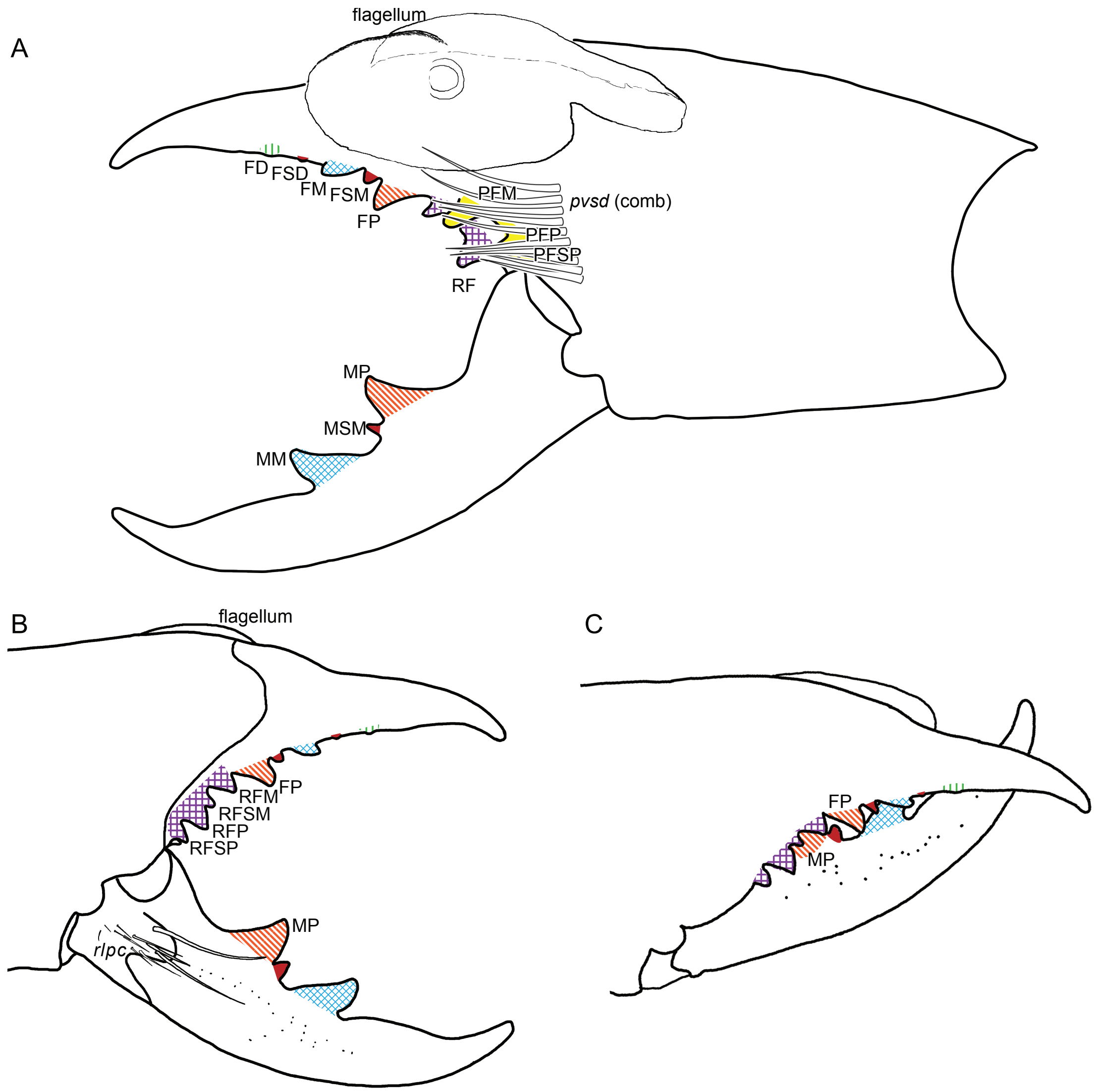

A
flagellum
FD
FSD
FM
FSM
FP
PFM
pvsd (comb)
PFP
PFSP
RF
MP
MSM
MM
B
flagellum
RFM
FP
RFSM
RFP
RFSP
rlpc
MP
C
FP
MP

PLATE 135. Daesiidae Kraepelin, 1899, *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]), chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellum. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger subdistal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

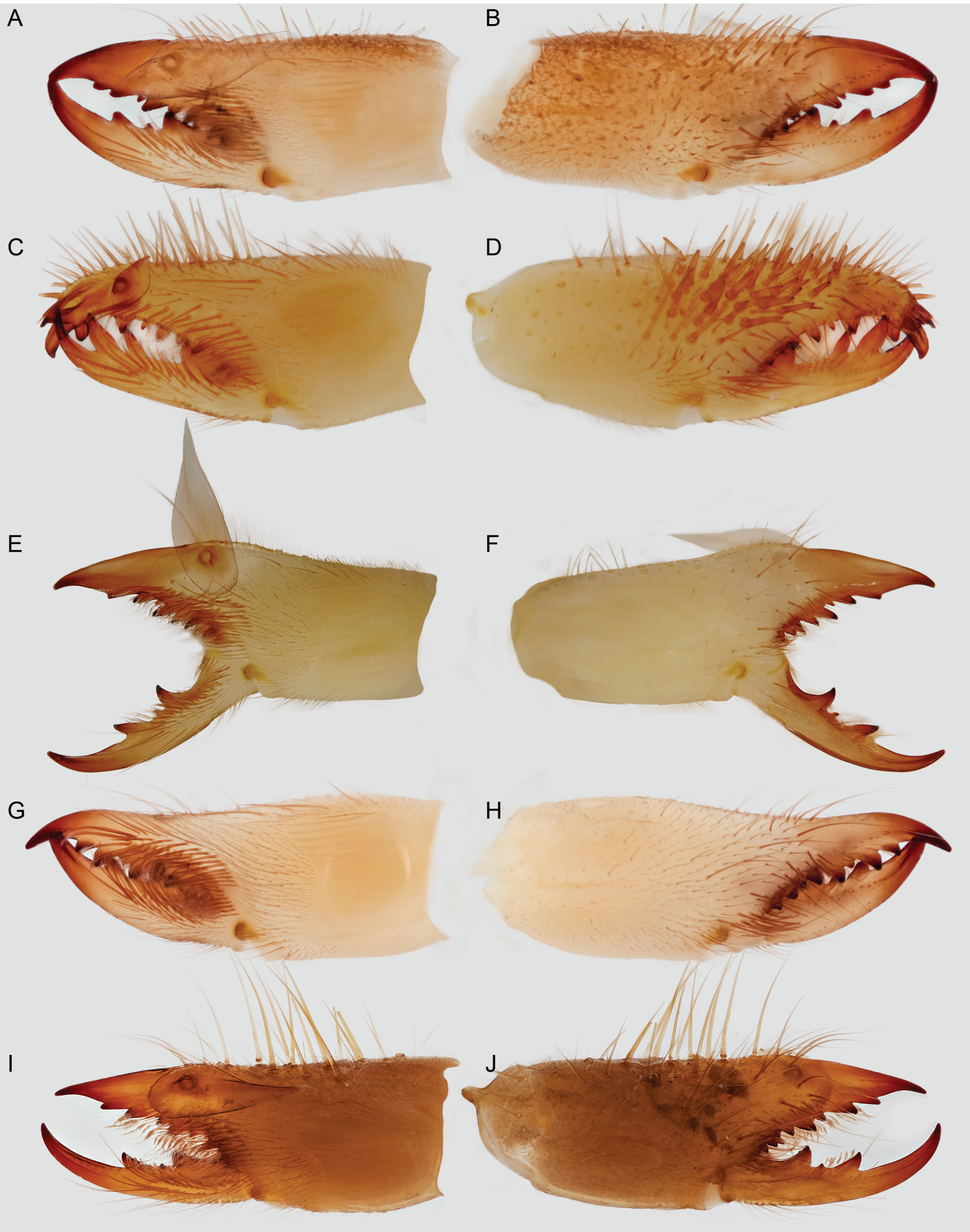


PLATE 136. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Gluviopsilla discolor* (Kraepelin, 1899), ♂ (AMNH [LP 7516]). **C, D.** *Gnosippus klunzingeri* Karsch, 1880, ♂ (HUJI 770). **E–H.** *Biton* (*B.*) *rossicus* (Birula, 1905). **E, F.** ♂ (AMNH [LP 3959]). **G, H.** ♀ (AMNH [LP 3959]). **I, J.** *Biton* (*B.*) *browni* (Lawrence, 1963), ♂ (AMNH [LP 3633]).

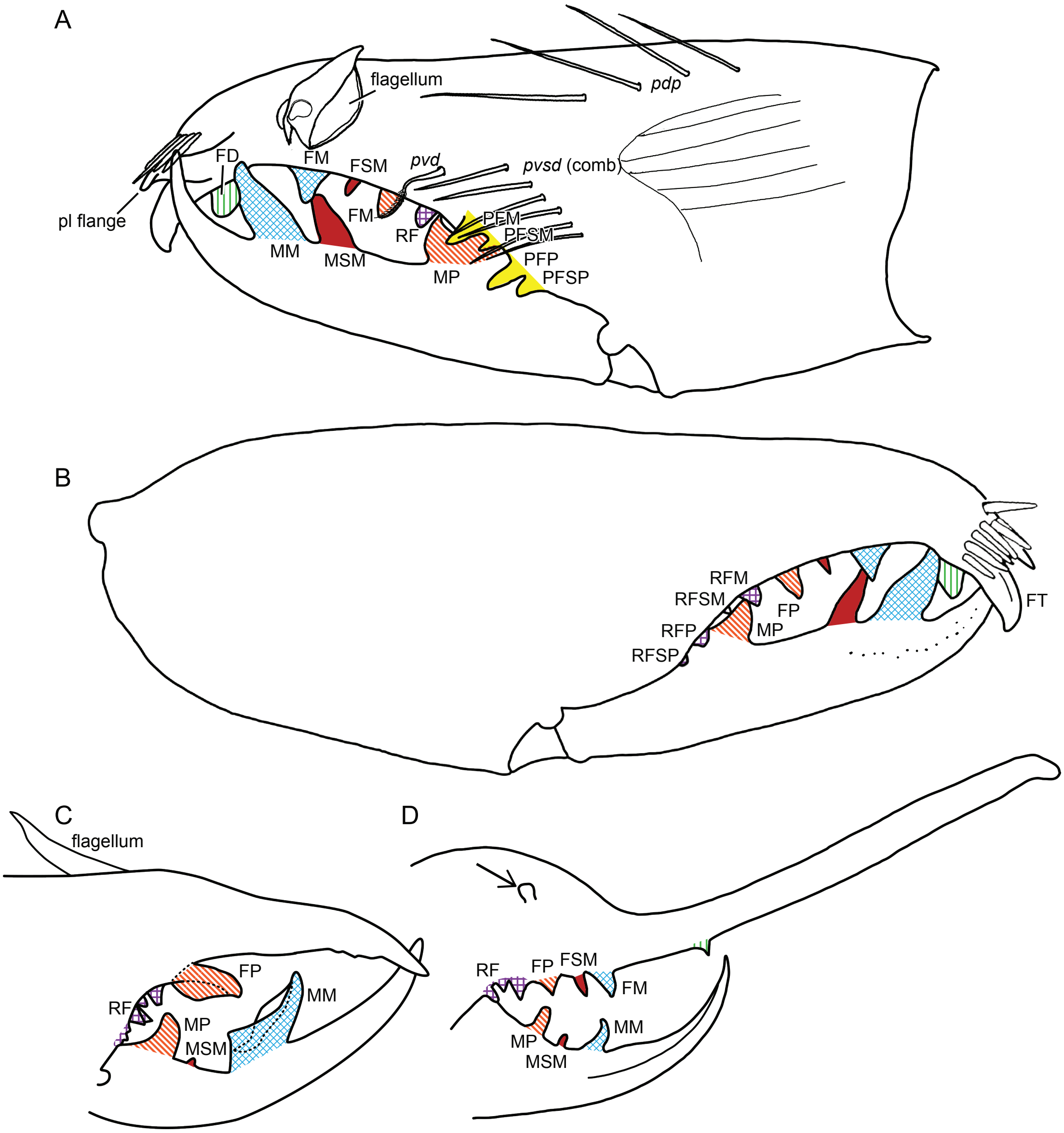

A
flagellum
pdp
FD
FM
FSM
pvd
pvsd (comb)
pl flange
FM
RF
PFM
PFSM
MM
MSM
MP
PFP
PFSP
B
RFM
RFSM
FP
RFP
MP
RFSP
FT
C
flagellum
FP
RF
MM
MP
MSM
D
RF
FP
FSM
FM
MM
MP
MSM

PLATE 137. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A**) and retrolateral (**B–D**) views, illustrating dentition, setae, and flagellum. **A, B.** *Gnosippus klunzingeri* Karsch, 1880, ♂ (HUJI 770). **C.** *Biton* (*B.*) *truncatidens* Lawrence, 1954, ♂, adapted from Lawrence (1954: 115, fig. 3D). **D.** *Ceratobiton styloceros* (Kraepelin, 1899), ♂ (HUJI 55), with elongated fixed finger. Arrow indicates flagellar attachment point visible retrolaterally through cuticle. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **FT,** fixed finger, terminal tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pdp,*** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **pl,** prolateral; ***pvd,*** proventral distal setae; ***pvsd,*** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

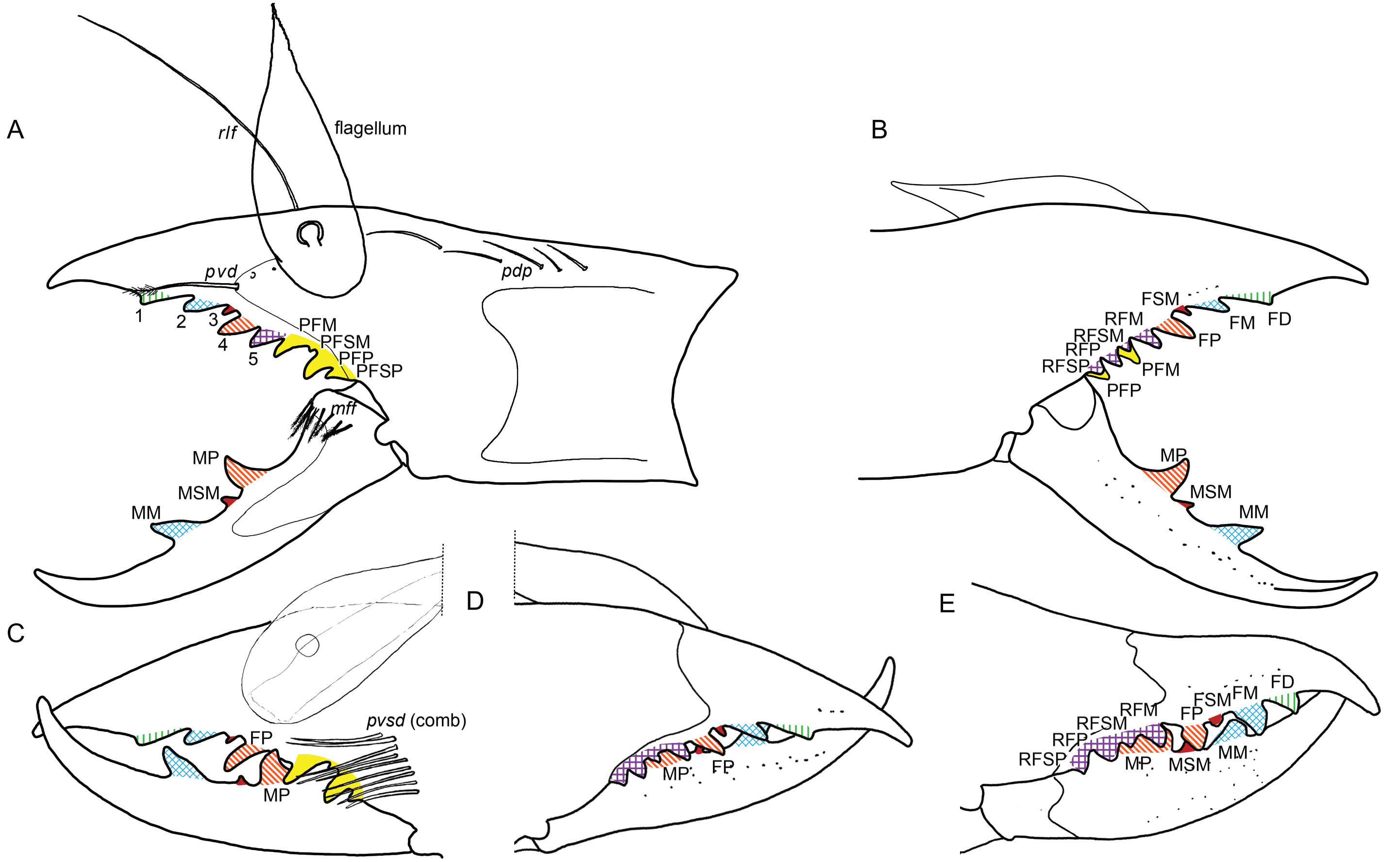

A
rlf
flagellum
pvd
pdp
1
2
3
4
5
PFM
PFSM
PFP
PFSP
mff
MP
MSM
MM
B
FSM
RFM
RFSM
RFP
RFSP
FM
FD
FP
PFM
PFP
MP
MSM
MM
C
FP
MP
pvsd (comb)
D
MP
FP
E
FSM
FM
FD
RFM
RFSM
RFP
RFSP
FP
MP
MSM
MM

PLATE 138. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B, D, E**) views, illustrating dentition, setae, and flagellum. **A–E.** *Biton* (*B.*) *rossicus* (Birula, 1905). **A–D.** ♂ (AMNH [LP 3959]). Numbers indicate five distalmost toothlike structures. **E.** ♀ (AMNH [LP 3959]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; ***mff,*** movable finger, fondal setae; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; ***pdp,*** prodorsal proximal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvd,*** proventral distal setae; ***pvsd,*** proventral subdistal setae (setal comb only); **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlf,*** retrolateral finger seta.

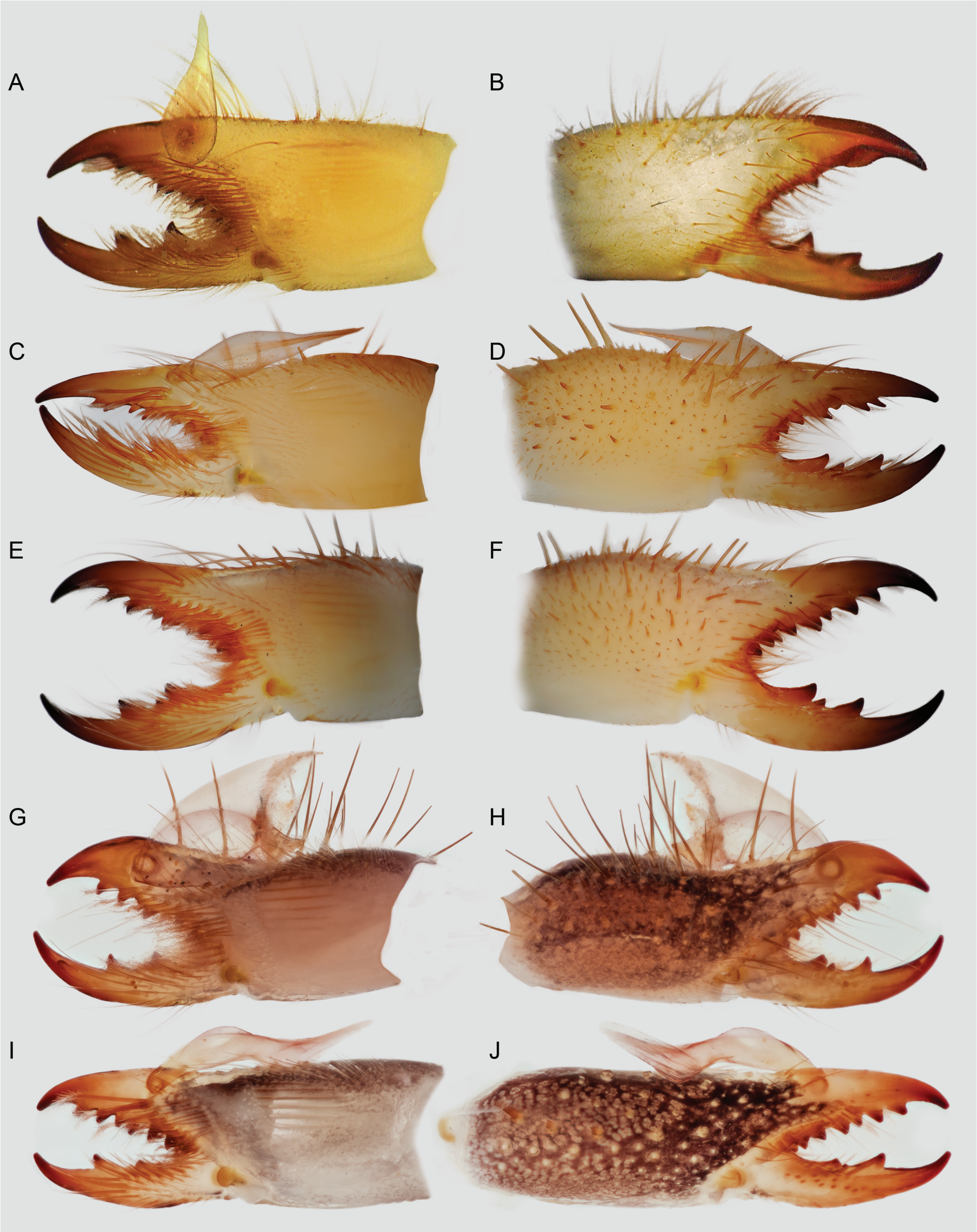
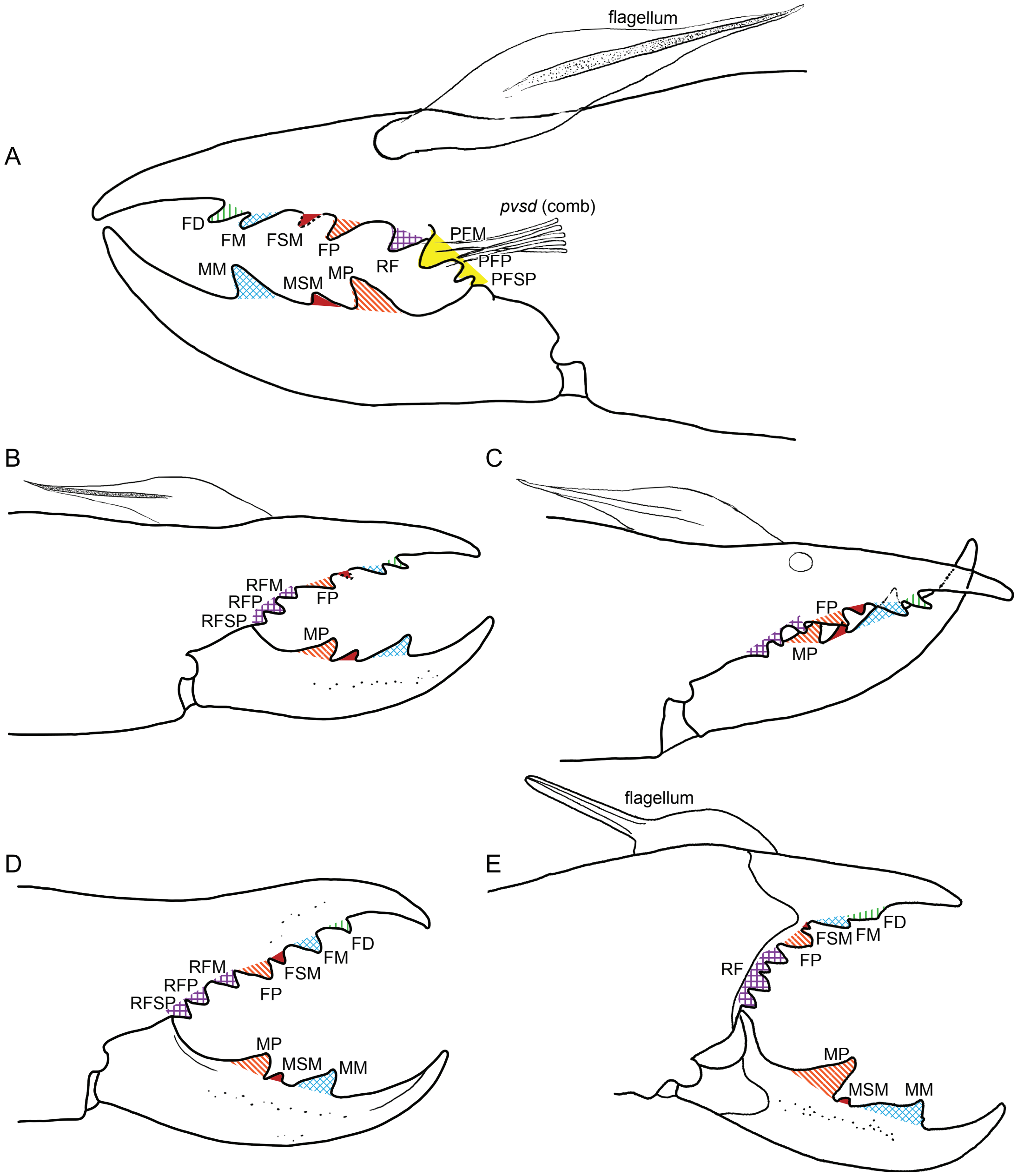


PLATE 139. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Biton* (*B.*) *zederbaueri* (Werner, 1905), ♂ (KUT), Turkey: Hasançali. **C–F.** *Blossia grandicornis* Lawrence, 1929. **C, D.** ♂ (AMNH [LP 5905]). **E, F.** ♀ (AMNH [LP 5905]). **G, H.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **I, J.** *Hemiblossia australis* (Purcell, 1902), ♂ (AMNH [LP 9866]).


A
flagellum
pvsd (comb)
FD
FM
FSM
FP
PFM
RF
PFP
PFSP
MM
MSM
MP
B
RFM
RFP
RFSP
FP
MP
C
FP
MP
D
RFM
RFP
RFSP
FD
FM
FSM
FP
MP
MSM
MM
E
flagellum
FD
FSM
FM
FP
RF
MP
MSM
MM

[PLATE 140. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A**) and retrolateral (**B–E**) views, illustrating dentition, setae, and flagellum. **A–D.** *Blossia grandicornis* Lawrence, 1929. **A–C.** ♂ (AMNH [LP 5905]). **D.** ♀ (AMNH [LP 5905]). **E.** *Biton* (*B.*) sp. 6 (*namaqua* group), ♂ (NMNW), Namibia: Windhoek, Auas Mountains. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth.

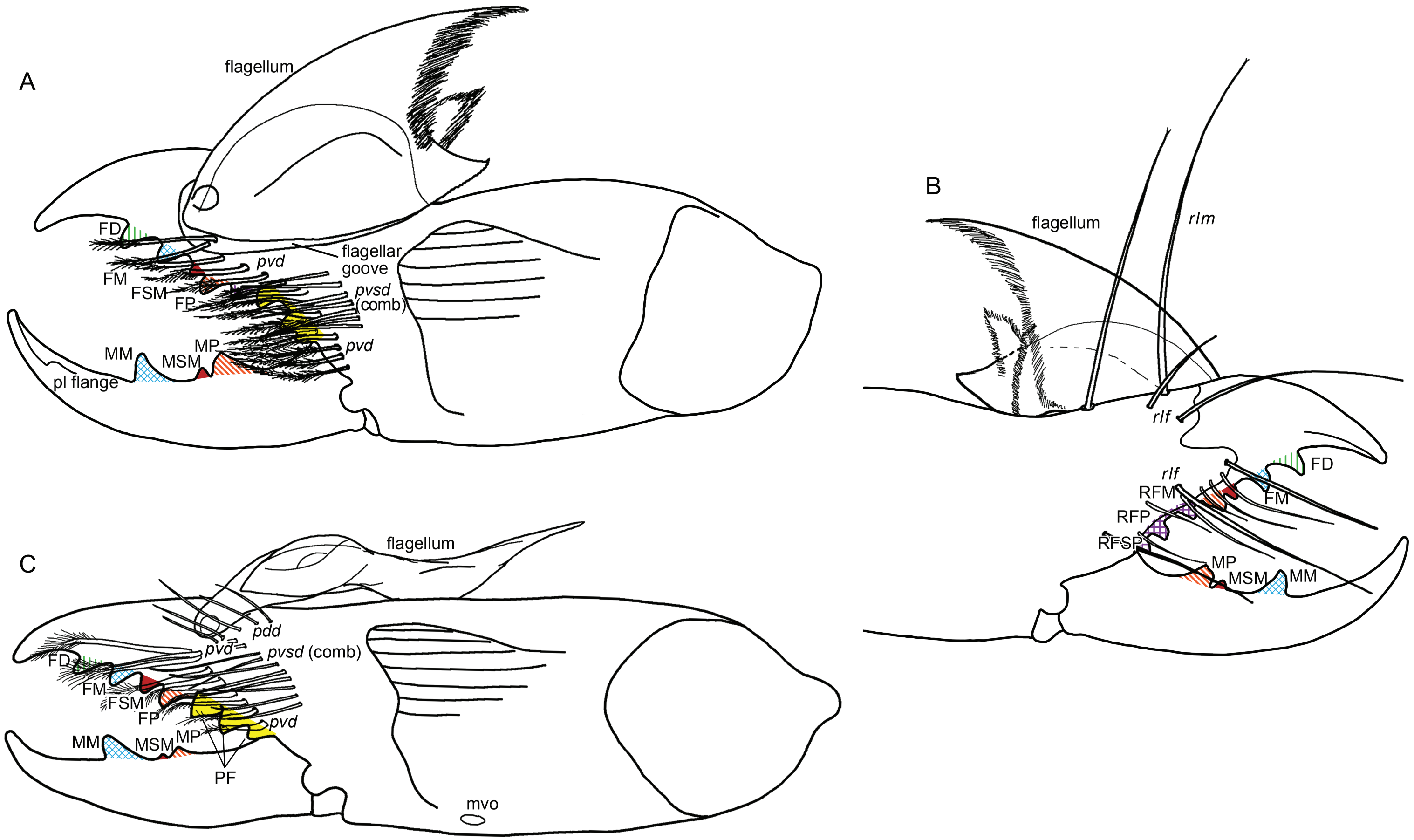

A
flagellum
FD
FM
FSM
FP
pvd
flagellar goove
pvsd (comb)
pvd
MM
MSM
MP
pl flange
B
flagellum
rlm
rlf
rlf
FD
FM
RFM
RFP
RFSP
MP
MSM
MM
C
flagellum
pdd
pvd
pvsd (comb)
FD
FM
FSM
FP
pvd
MM
MSM
MP
PF
mvo

PLATE 141. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B**) views, illustrating dentition, setae, and flagellum. **A, B.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **C.** *Hemiblossia australis* (Purcell, 1902), ♂ (AMNH [LP 9866]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **mvo,** medioventral organ; ***pdd*,** prodorsal distal setae; **PF,** profondal teeth; ***pvd*,** proventral distal setae; **pl,** prolateral; ***pvsd*,** proventral subdistal setae (setal comb only); **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth; ***rlf*,** retrolateral finger setae; ***rlm*,** retrolateral manus setae.

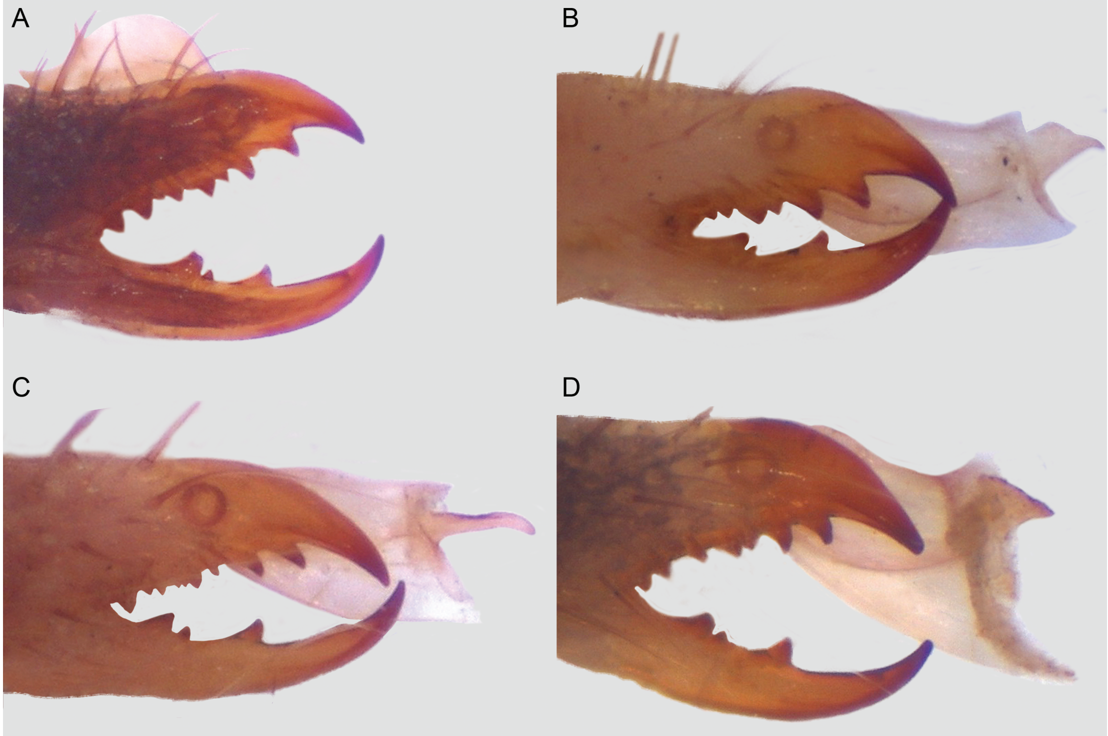


PLATE 142. Daesiidae Kraepelin, 1899, chelicerae, retrolateral views. **A.** *Hemiblossia oneili* Purcell, 1902, ♂ (NMNW), Namibia: Gondwana Cañon Park. **B, C.** *Hemiblossia* spp. (*bouvieri* group), sp. 1, 2, ♂ (NMNW), Namibia: Gondwana Cañon Park. **D.** *Hemiblossia etosha* Lawrence, 1927, ♂ (NMNW 13798).

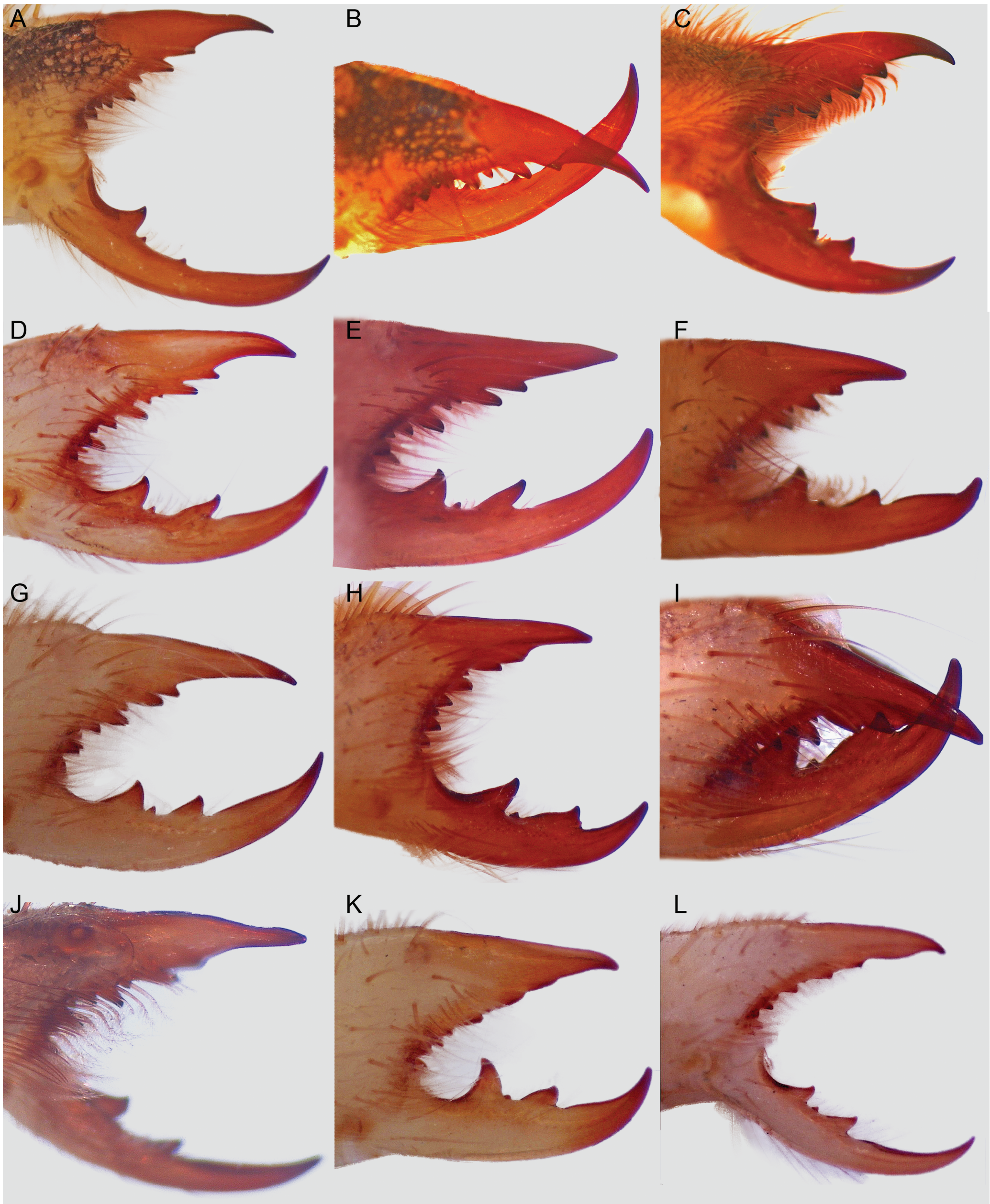


PLATE 143. Daesiidae Kraepelin, 1899, chelicerae, retrolateral (**A–I, K, L**), and prolateral (**J**) views. **A, B.** *Biton* (*B.*) sp. 1, ♂ (NMNW 13278). **C.** *Biton* (*B.*) sp. 1, ♀ (NMNW 13278). **D.** *Biton* (*B.*) sp. 2, ♂ (NMNW), Namibia: Gondwana Cañon Park, with two fixed finger, submedial (FSM) teeth (within same collecting series, one specimen with single FSM on both chelicerae). **E.** *Biton* (*B.*) sp. 3, ♂ (AMNH [LP 9852]), left chelicera with two FSM, right chelicera (not shown) with single FSM. **F.** *Biton* (*B.*) sp. 4, ♂ (NMNW), Namibia: Gondwana Cañon Park. **G.** *Biton* (*B.*) sp. 5, ♂ (NMNW 12228). **H, I.** *Biton* (*B.*) sp. 6 (*namaqua* group), ♂ (NMNW), Namibia: Windhoek, Auas Mountains. **J.** *Biton* (*B.*) sp. 7, ♂ (AMNH [LP 9853]). **K.** *Biton* (*B.*) sp. 8, ♂ (NMNW 12336). **L.** *Eberlanzia flava* Roewer, 1941, ♂ (NMNW 11175).

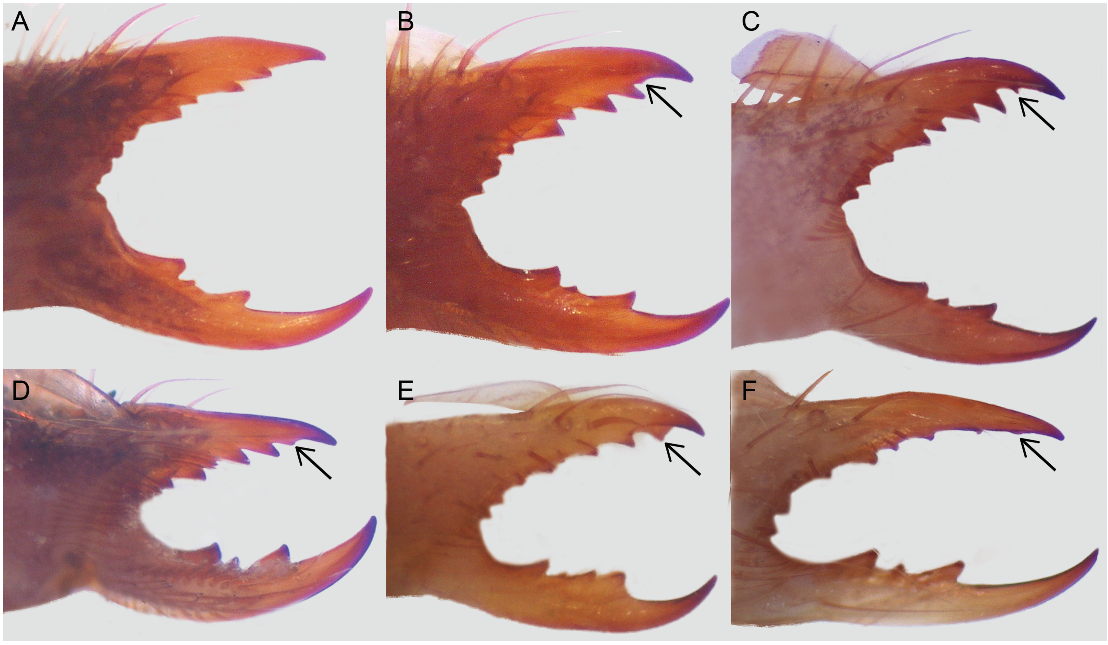


PLATE 144. Daesiidae Kraepelin, 1899, chelicerae, retrolateral (**A–C, E, F**), and prolateral (**D**) views. **A.** *Blossia* sp., ♂ (NMNW), Namibia: Namib-Naukluft Park. **B.** *Blossia tricolor* Hewitt, 1914, ♂ (NMNW), Namibia: Gondwana Cañon Park. **C.** *Blossia* cf. *purpurea*, ♂ (NMNW 13893). **D.** *Blossia spinicornis* Lawrence, 1928, ♂ (NMNW), Namibia: Windhoek. **E.** *Blossia* cf. *rooica*, ♂ (NMNW), Namibia: Gondwana Cañon Park. **F.** *Blossia sabulosa* (Lawrence, 1972), ♂ (NMNW), Namibia: Namib-Naukluft Park. Arrows indicate subterminal flange.

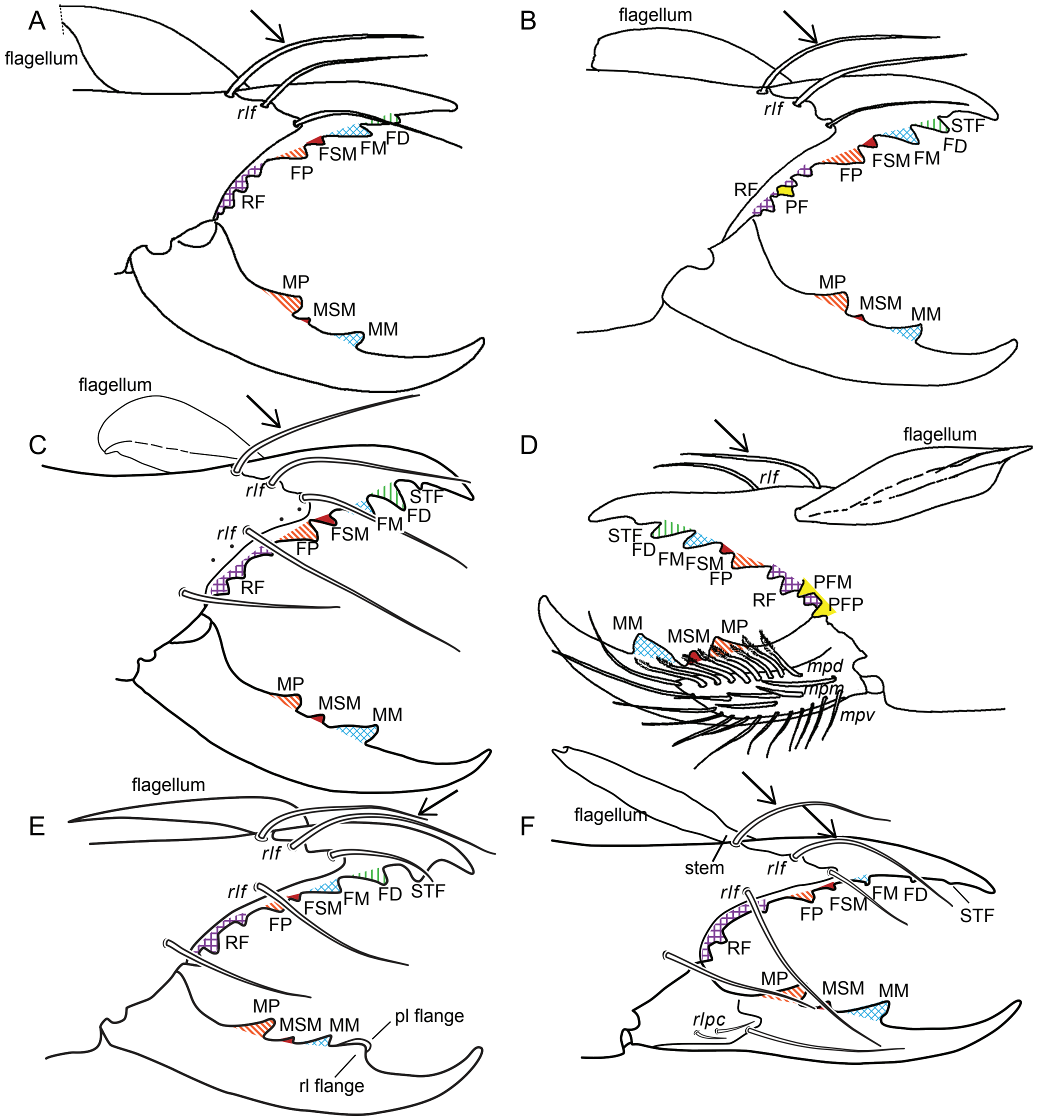

A
flagellum
rlf
FD
FM
FSM
FP
RF
MP
MSM
MM
B
flagellum
rlf
STF
FD
FM
FSM
FP
RF
PF
MP
MSM
MM
flagellum
C
rlf
STF
FD
FM
rlf
FSM
FP
RF
MP
MSM
MM
D
flagellum
rlf
STF
FD
FM
FSM
FP
PFM
RF
PFP
MM
MSM
MP
mpd
mpm
mpv
flagellum
E
rlf
rlf
FM
FD
STF
FSM
FP
RF
MP
MSM
MM
pl flange
rl flange
flagellum
F
stem
rlf
rlf
FM
FD
FP
FSM
STF
RF
MP
MSM
MM
rlpc

PLATE 145. Daesiidae Kraepelin, 1899, chelicerae, retrolateral (**A–C, E, F**), and prolateral (**D**) views, illustrating dentition, setae, and flagellum. **A.** *Blossia* sp., ♂ (NMNW), Namibia: Namib-Naukluft Park. **B.** *Blossia tricolor* Hewitt, 1914, ♂ (NMNW), Namibia: Gondwana Cañon Park. **C.** *Blossia* cf. *purpurea*, ♂ (NMNW 13893). **D.** *Blossia spinicornis* Lawrence, 1928, ♂ (NMNW), Namibia: Windhoek. **E.** *Blossia* cf. *rooica*, ♂ (NMNW), Namibia: Gondwana Cañon Park, with prolateral and retrolateral flanges forming toothlike structure distal to MM tooth. **F.** *Blossia sabulosa* (Lawrence, 1972), ♂ (NMNW), Namibia: Namib-Naukluft Park. Arrows indicate modified *rlf* (i.e., *principal rlf*). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; ***mpd*,** movable finger, prodorsal setae; ***mpm*,** movable finger, promedial setae; ***mpv*,** movable finger, proventral setae; **MSM,** movable finger, submedial tooth; **PF,** profondal teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **pl,** prolateral; **RF,** retrofondal teeth; **rl,** retrolateral; ***rlf*,** retrolateral finger setae; ***rlpc*,** retrolateral proximal setal cluster; **STF,** subterminal flange.

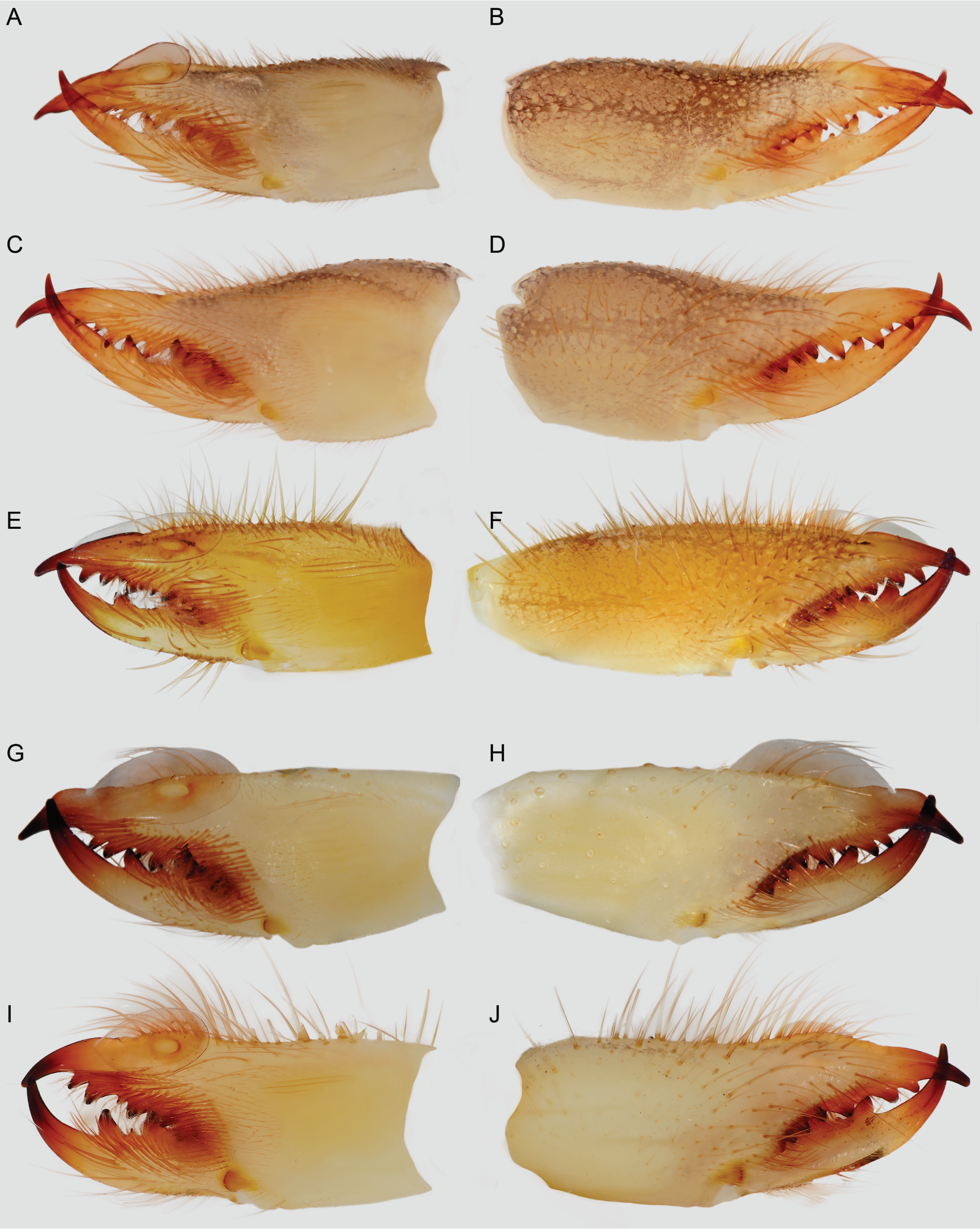


PLATE 146. Ammotrechidae Roewer, 1934, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Pseudocleobis andinus* (Pocock, 1899). **A, B.** ♂ (AMNH [LP 2384]). **C, D.** ♀ (AMNH [LP 2384]). **E, F.** *Ammotrecha stollii* (Pocock, 1895), ♂ (AMNH [LP 8605]). **G, H.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]). **I, J.** *Oltacola gomezi* Roewer, 1932, ♂ (AMNH [LP 2262A]).

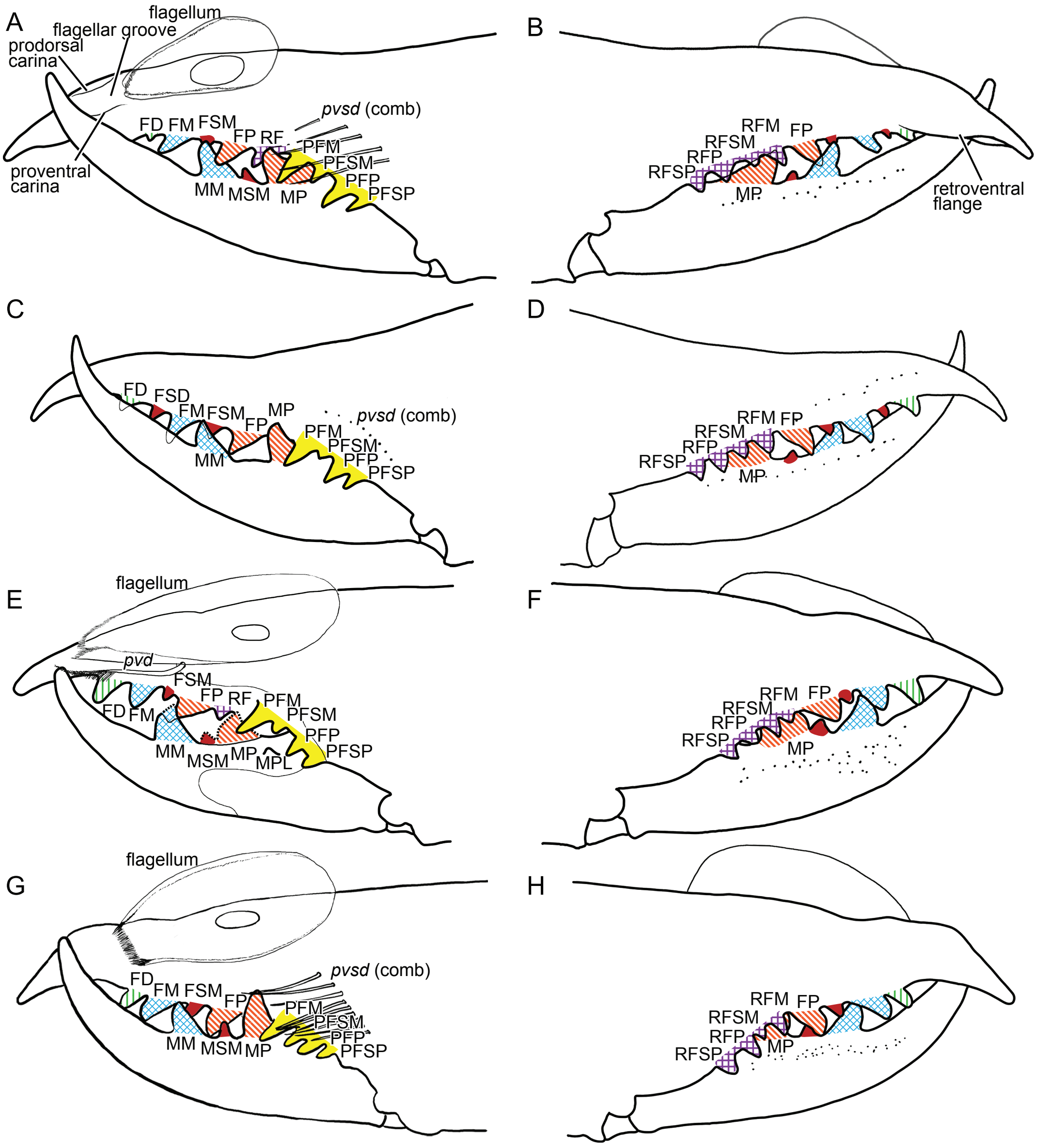

A
flagellum
flagellar groove
prodorsal carina
proventral carina
FD FM FSM
FP RF
pvsd (comb)
PFM
PFSM
PFP
PFSP
MM MSM MP
B
RFM FP
RFSM
RFP
RFSP
MP
retroventral flange
C
FD FSD
FM FSM
MP
FP
pvsd (comb)
PFM
PFSM
PFP
PFSP
MM
D
RFM FP
RFSM
RFP
RFSP
MP
E
flagellum
pvd
FSM
FP RF PFM
PFSM
FD FM
PFP
PFSP
MM MSM MP MPL
F
RFM FP
RFSM
RFP
RFSP
MP
G
flagellum
pvsd (comb)
FD
FM FSM
FP
PFM
PFSM
PFP
PFSP
MM MSM MP
H
RFM FP
RFSM
RFP
RFSP
MP

PLATE 147. Ammotrechidae Roewer, 1934, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views, illustrating dentition, setae, and flagellum. **A–D.** *Pseudocleobis andinus* (Pocock, 1899). **A, B.** ♂ (AMNH [LP 2384]). **C, D.** ♀ (AMNH [LP 2384]). **E, F.** *Ammotrecha stollii* (Pocock, 1895), ♂ (AMNH [LP 8605]). **G, H.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MPL,** movable finger, prolateral tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvd*,** proventral distal (apicalmost setae only); ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

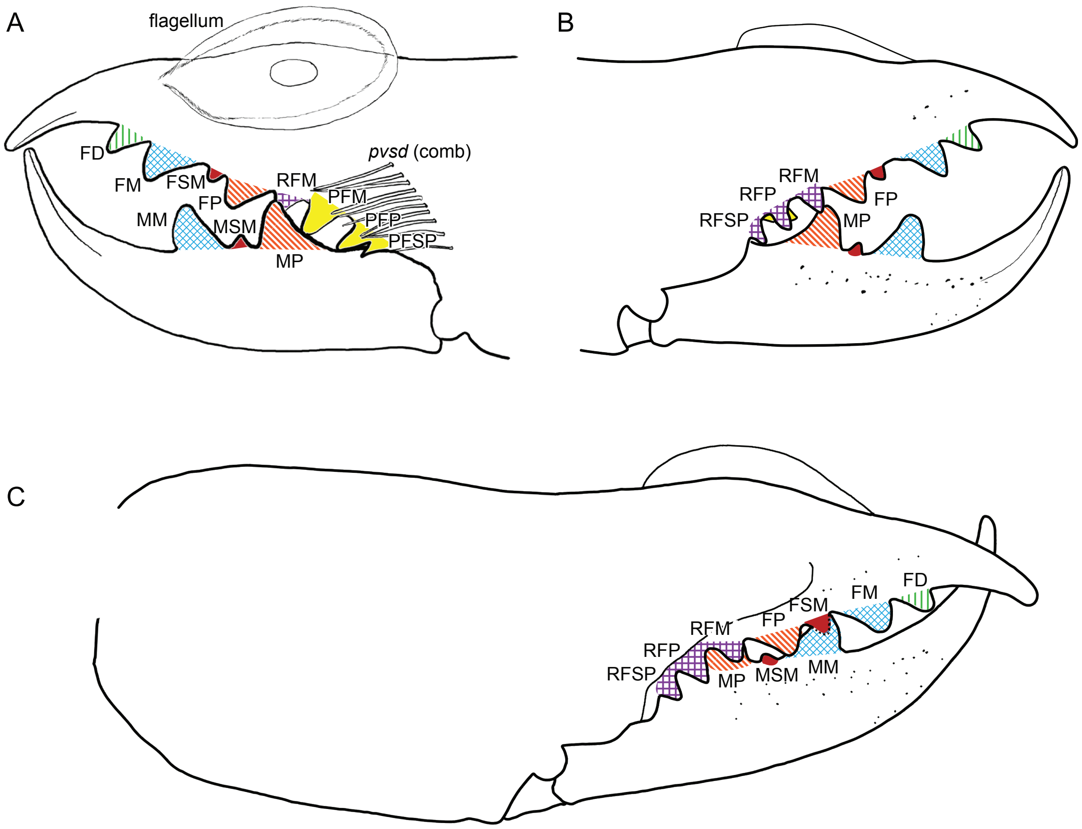

A
flagellum
pvsd (comb)
FD
FM
FSM
FP
RFM
PFM
MM
MSM
PFP
PFSP
MP
B
RFM
RFP
RFSP
FP
MP
C
FD
FM
FSM
FP
RFM
RFP
RFSP
MP
MSM
MM

PLATE 148. Ammotrechidae Roewer, 1934, chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, indicating dentition, setae, and flagellum. **A–C.** *Oltacola gomezi* Roewer, 1932. **A, B.** ♂ (AMNH [LP 2262A]), with cheliceral fingers open. **C.** ♂ (AMNH [LP 10681]), with fingers closed, illustrating shape of chelicera and indistinct margin of sclerotized area on fixed finger. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth.

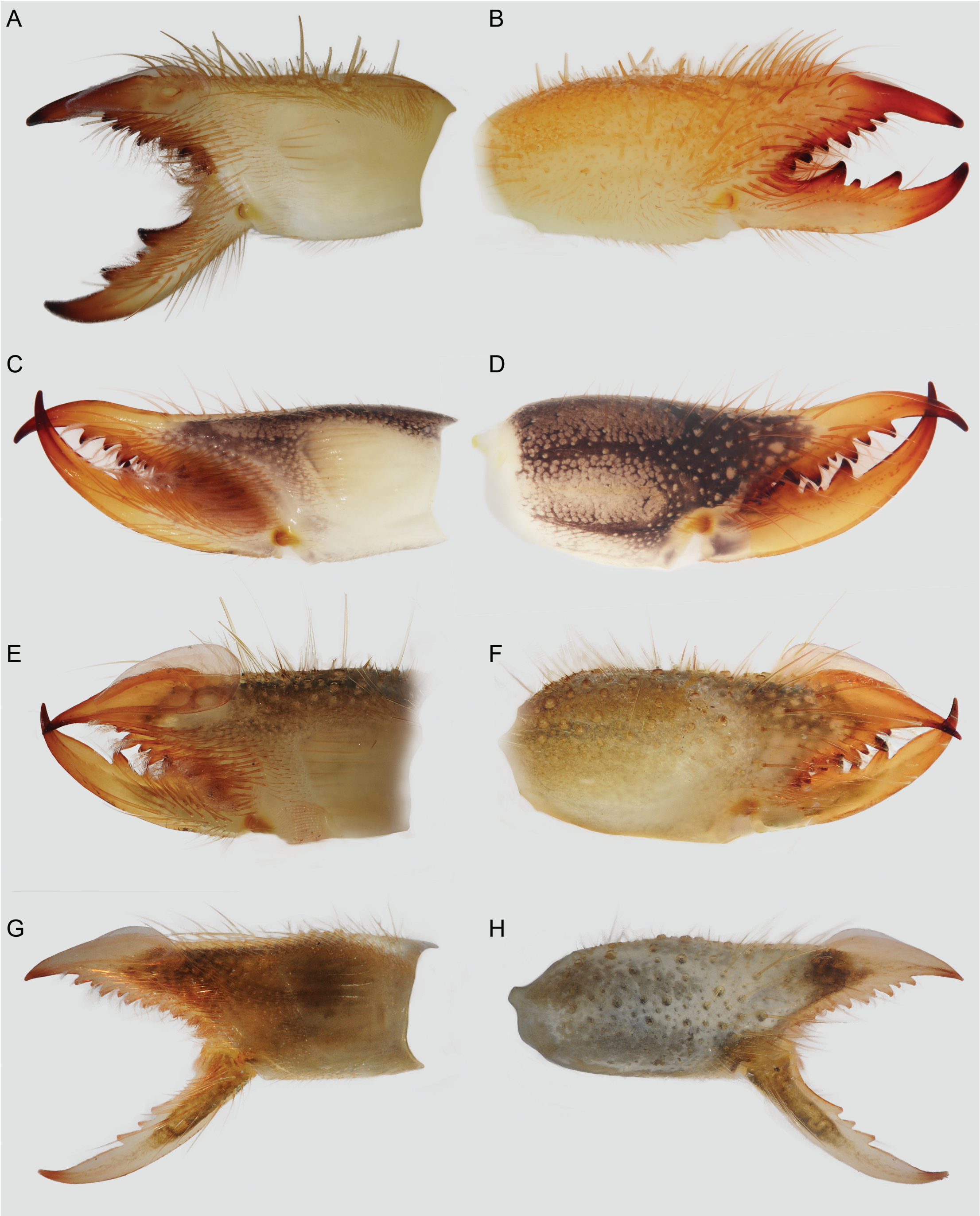


PLATE 149. Ammotrechidae Roewer, 1934 (**A–D**) and Mummuciidae Roewer, 1934 (**E–H**), chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **C, D.** *Sedna pirata* Muma, 1971, ♀ (AMNH [LP 2362]). **E, F.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]). **G, H.** *Uspallata* cf. *pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]).

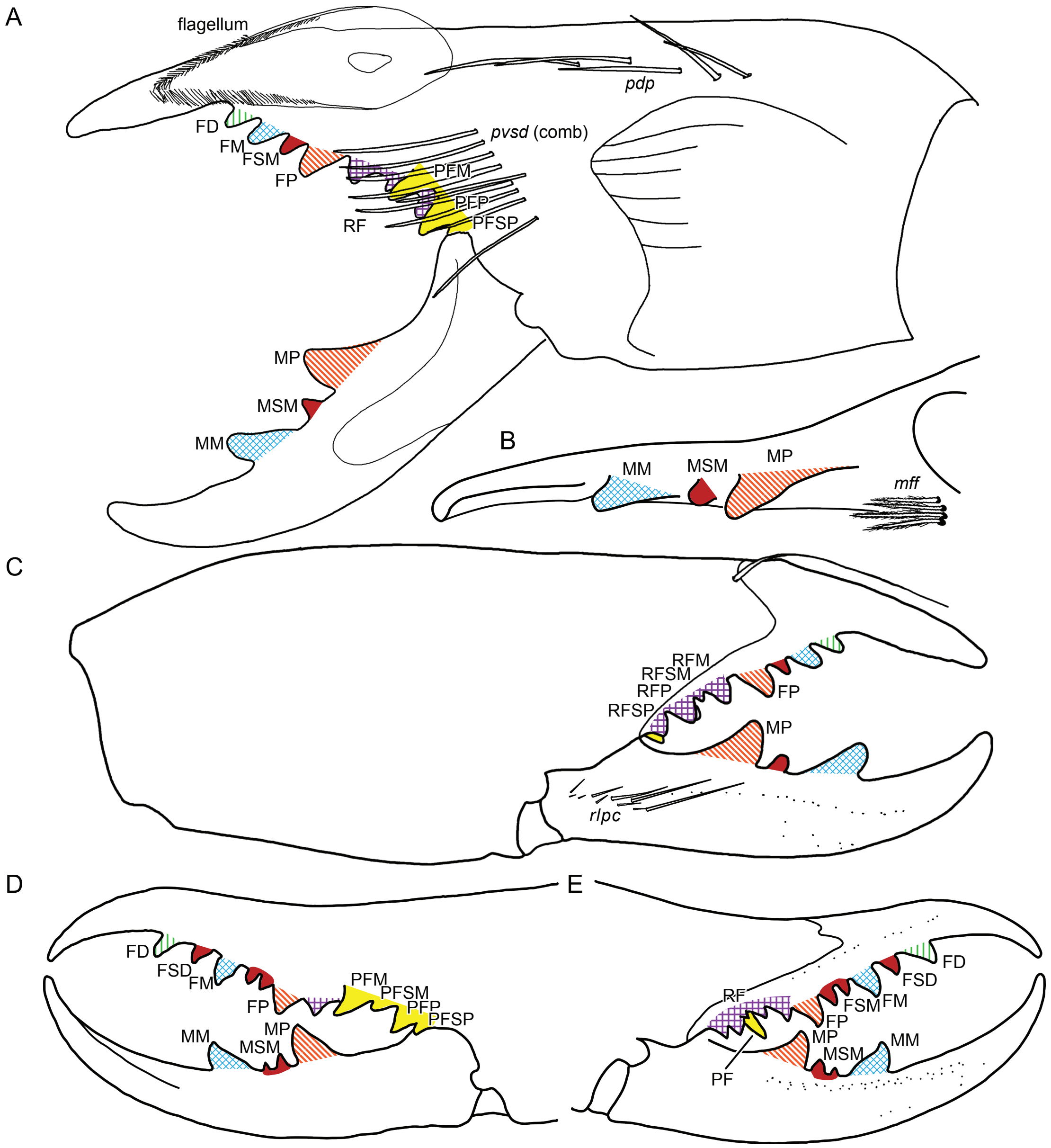

A
flagellum
pdp
pvsd (comb)
FD
FM
FSM
FP
PFM
PFP
PFSP
RF
MP
MSM
MM
B
MM
MSM
MP
mff
C
RFM
RFSM
RFP
RFSP
FP
MP
rlpc
D
FD
FSD
FM
FP
PFM
PFSM
PFP
PFSP
MM
MP
MSM
E
FD
FSD
FSM
FM
RF
FP
MP
MSM
MM
PF

PLATE 150. Ammotrechidae Roewer, 1934, chelicerae, prolateral (**A**) and retrolateral (**C–E**) views, and movable finger, retrodorsal view (**B**), illustrating dentition, setae, and flagellum. **A–C.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). Flagellum not shown in **C. D, E.** *Sedna pirata* Muma, 1971, ♀ (AMNH [LP 2362]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial teeth; ***mff*,** movable finger, fondal setae; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; ***pdp*,** prodorsal proximal setae; **PF,** profondal teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster.

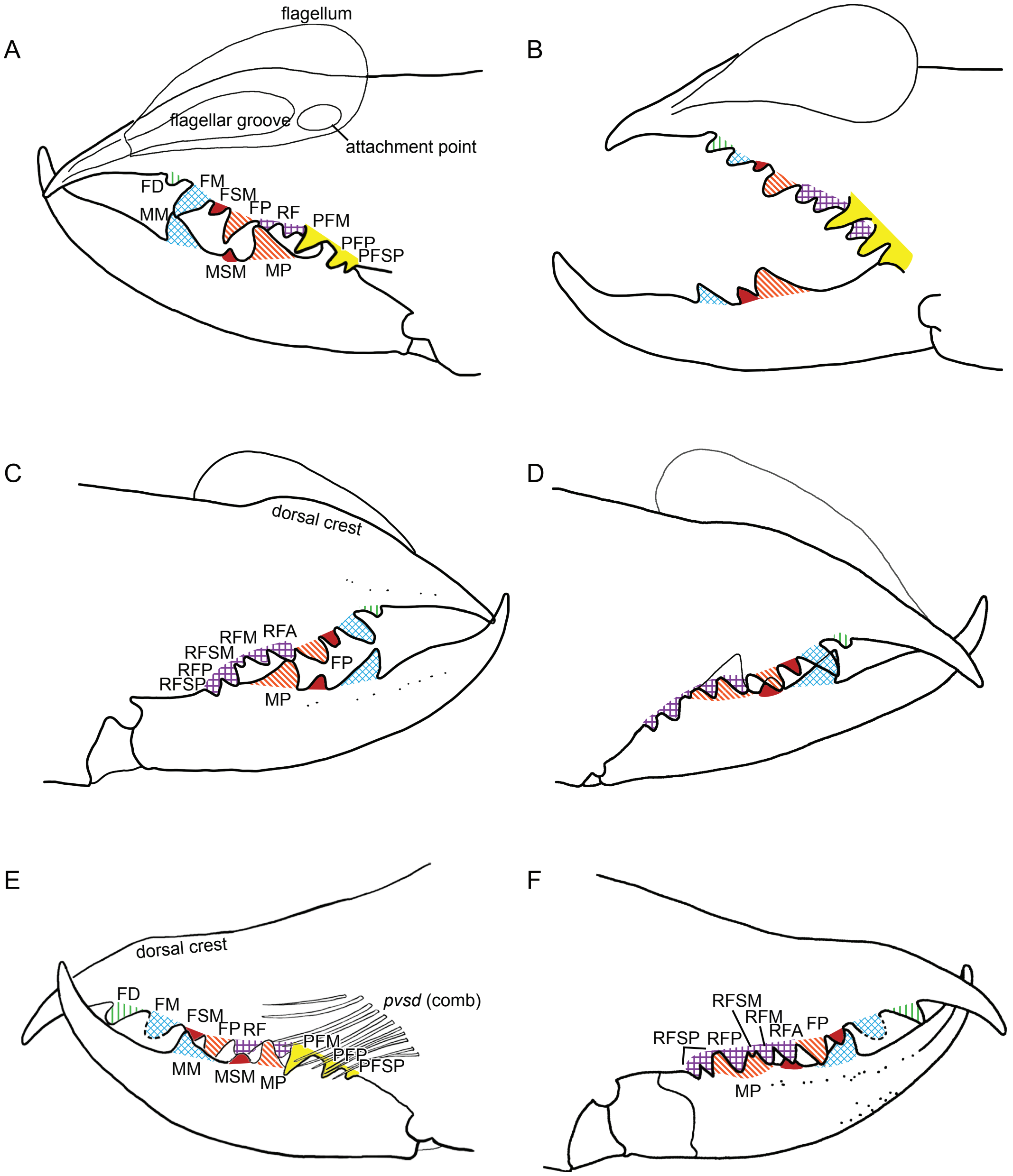

A
flagellum
flagellar groove
attachment point
FD
FM
FSM
MM
FP
RF
PFM
PFP
PFSP
MSM
MP
B
C
dorsal crest
RFM
RFA
RFSM
RFP
RFSP
FP
MP
D
E
dorsal crest
FD
FM
FSM
FP
RF
pvsd (comb)
PFM
PFP
PFSP
MM
MSM
MP
F
RFSM
RFM
RFA
FP
RFSP
RFP
MP

PLATE 151. Mummuciidae Roewer, 1934, chelicerae, prolateral (**A, B, E**) and retrolateral (**C, D, F**) views, illustrating dentition, setae, and flagellum. **A–F.** *Gaucha fasciata* Mello-Leitão, 1924. **A, C, D.** ♂ (AMNH [LP 5858). **B.** ♂, adapted from Maury (1970: 360, fig. 2). **E, F.** ♀ (AMNH [LP 10699]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

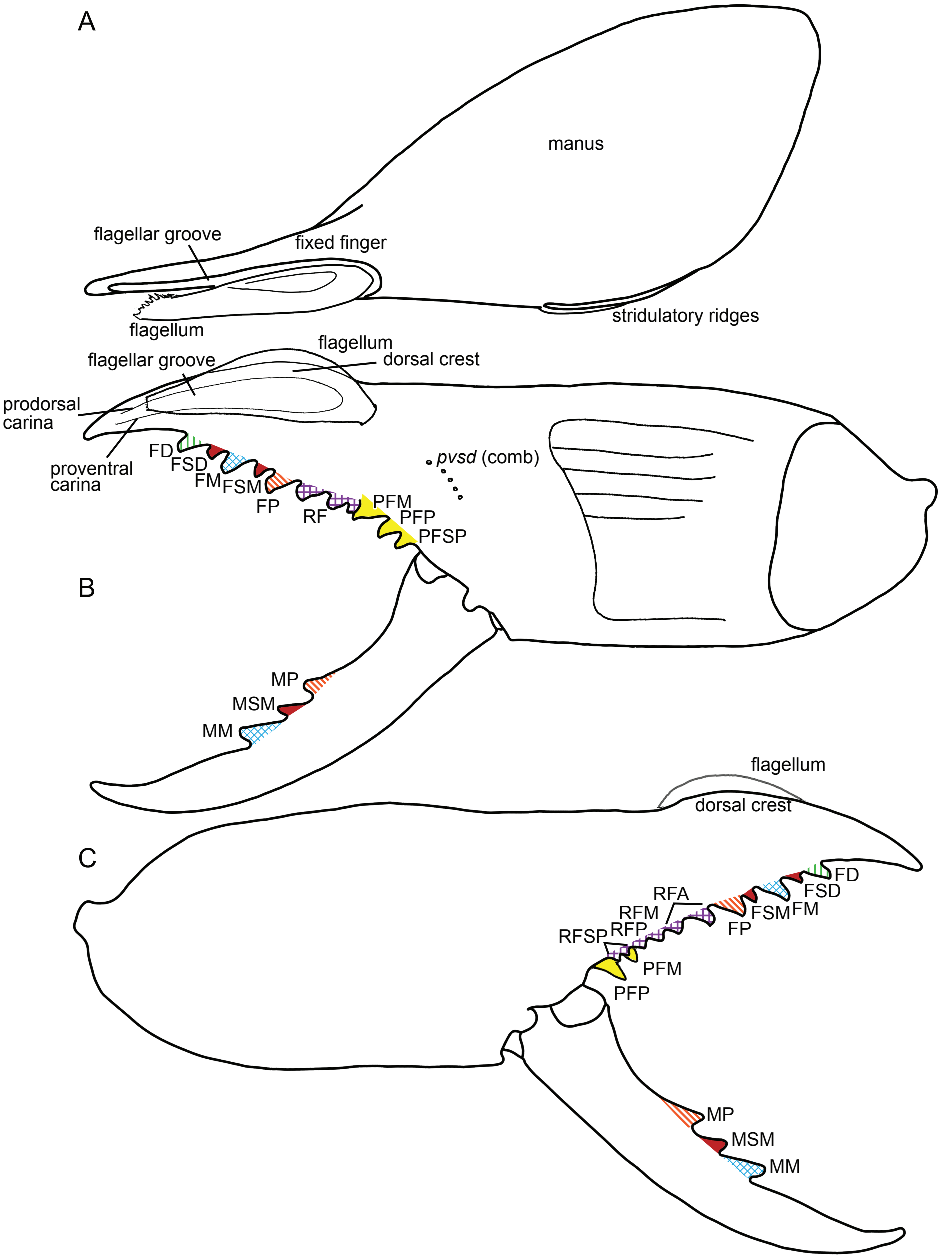

A
manus
flagellar groove
fixed finger
flagellum
stridulatory ridges
flagellum
flagellar groove
dorsal crest
prodorsal carina
proventral carina
FD
FSD
FM
FSM
FP
RF
PFM
PFP
PFSP
pvsd (comb)
B
MP
MSM
MM
flagellum
dorsal crest
C
FD
FSD
FM
FSM
FP
RFA
RFM
RFP
RFSP
PFM
PFP
MP
MSM
MM

PLATE 152. Mummuciidae Roewer, 1934, *Uspallata* cf. *pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]), chelicerae, dorsal (**A**), prolateral (**B**), and retrolateral (**C**) views, illustrating dentition, setae, and flagellum. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RF,** retrofondal teeth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth.

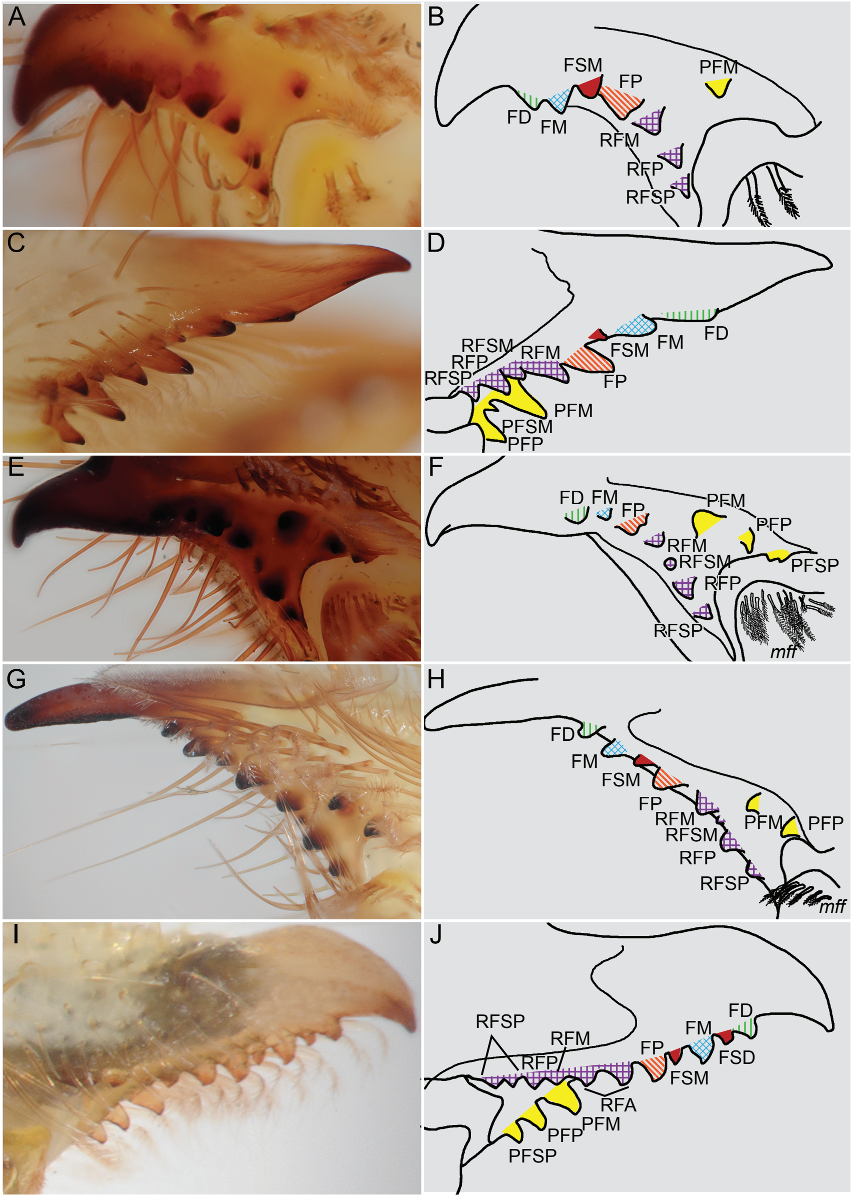

A
B
FSM
FP
PFM
FD
FM
RFM
RFP
RFSP
C
D
RFSM
RFP
RFSP
RFM
FSM
FM
FD
FP
PFM
PFSM
PFP
E
F
FD
FM
FP
PFM
PFP
RFM
RFSM
PFSP
RFP
RFSP
mff
G
H
FD
FM
FSM
FP
RFM
RFSM
RFP
RFSP
PFM
PFP
mff
I
J
RFSP
RFM
RFP
FP
FM
FD
FSD
FSM
RFA
PFM
PFP
PFSP

PLATE 153. Daesiidae Kraepelin, 1899 (**A–F**), Ammotrechidae Roewer, 1934 (**G, H**), and Mummuciidae Roewer, 1934 (**I, J**), cheliceral fixed fingers, proventral (**A, B, E–H**) and retroventral (**C, D, I, J**) views, illustrating fondal area. **A, B.** *Blossia grandicornis* Lawrence, 1929, ♂ (AMNH [LP 5905]). **C, D.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♂ (AMNH [LP 3959]). **E, F.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **G, H.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **I, J.** *Uspallata* cf. *pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; ***mff*,** movable finger, fondal setae; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSM,** profondal submedial tooth; **PFSP,** profondal subproximal tooth; **RFA,** retrofondal apical teeth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal tooth.

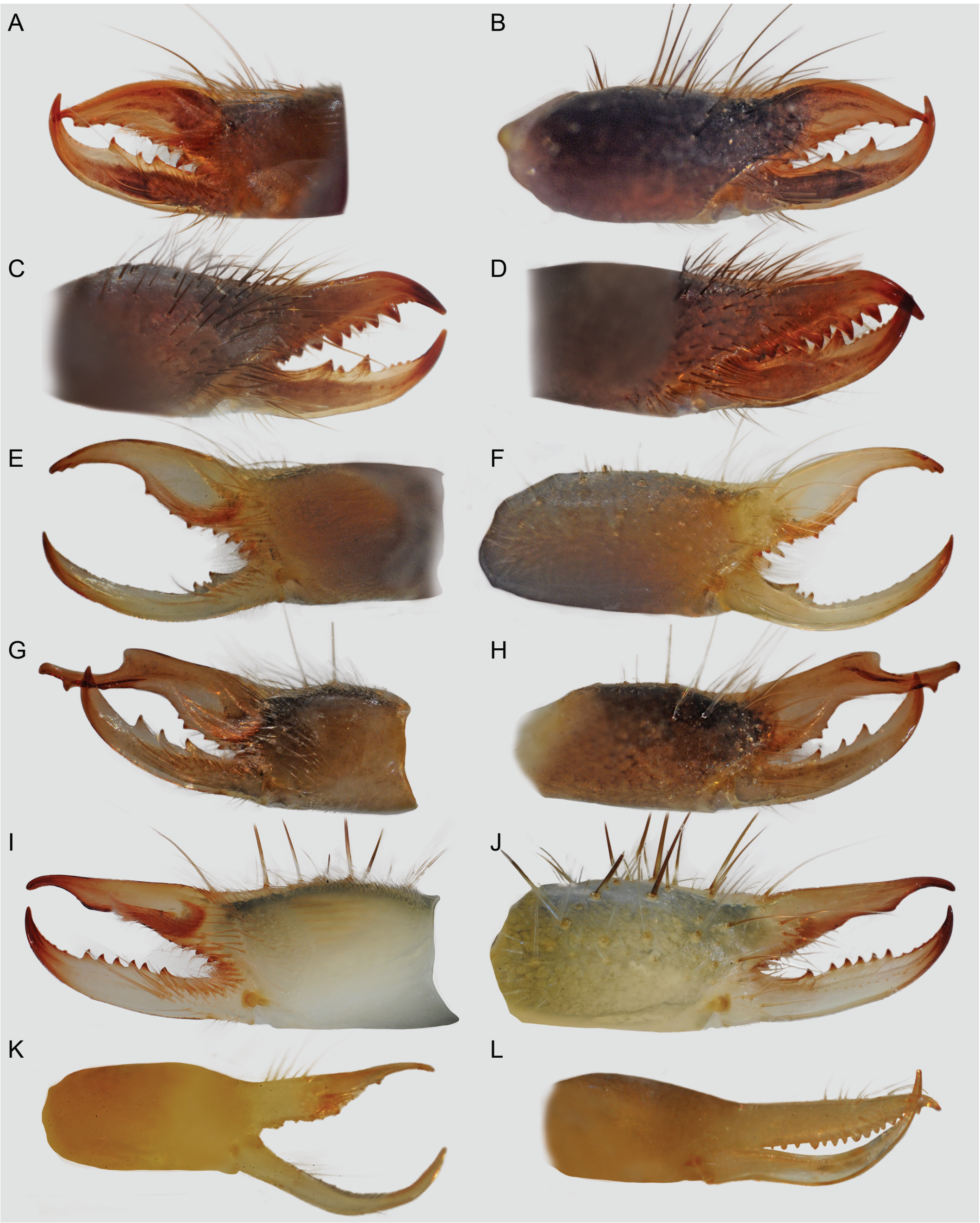


PLATE 154. Melanoblossiinae Roewer, 1933, chelicerae, prolateral (**A, E, G, I**) and retrolateral (**B–D, F, H, J–L**), views. **A–D.** *Melanoblossia braunsi*, Purcell, 1903. **A, B** ♂ (AMNH [LP 10737]). **C, D.** ♀ (AMNH [LP 10737]), sinistral chelicera (mirror image) with bifid (**C**), and dextral chelicera with regular (**D**) fixed finger medial (FM) tooth. **E, F.** *Melanoblossia* cf. *braunsi*, ♂ (AMNH [LP 8550]). **G, H.** *Melanoblossia* sp., ♂ (AMNH [LP 9857]). **I, J.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). **K, L.** *Lawrencega minuta* Wharton, 1981. **K.** Paratype ♂ (CAS 9033898). **L.** Paratype ♀ (CAS 9033898).

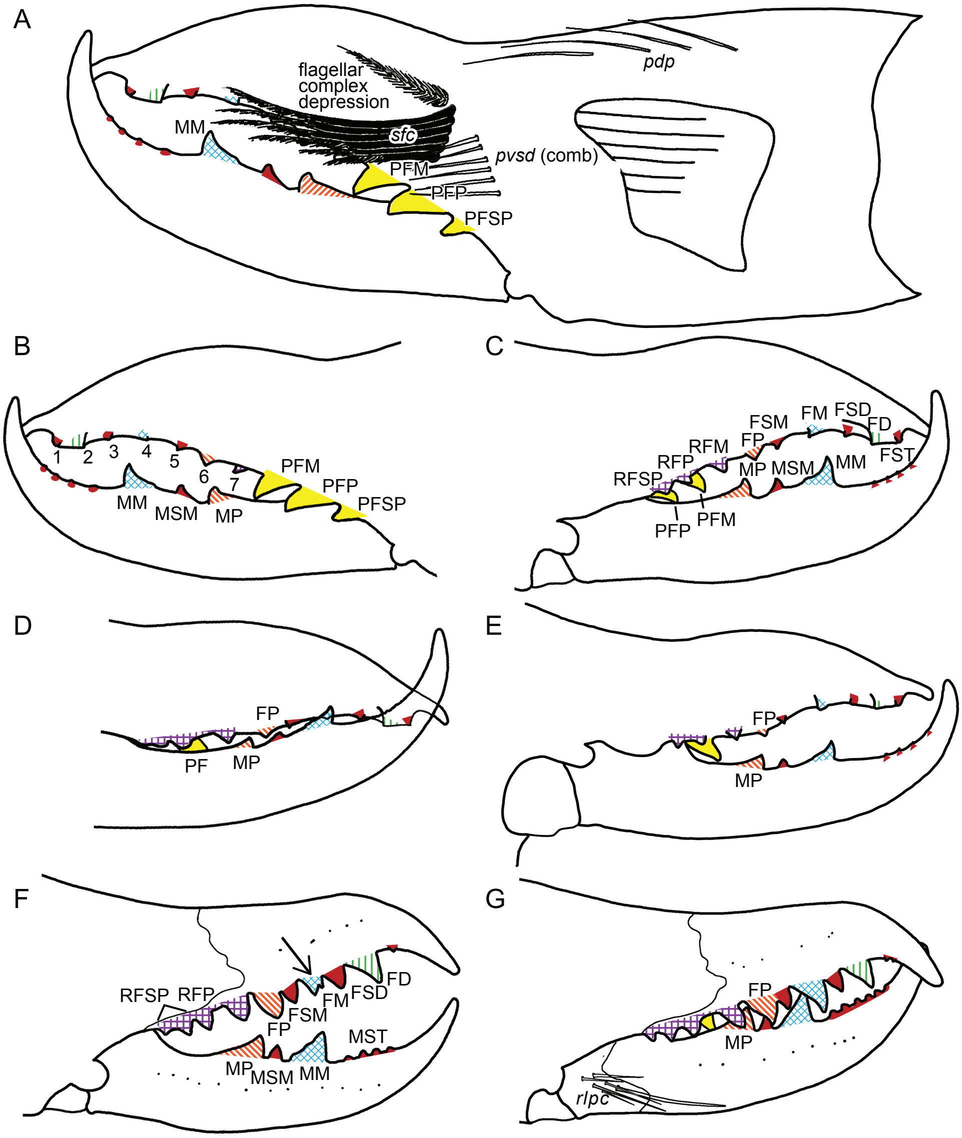

A
flagellar complex depression
pdp
MM
sfc
pvsd (comb)
PFM
PFP
PFSP
B
1
2
3
4
5
6
7
MM
MSM
MP
PFM
PFP
PFSP
C
FSM
FM
FSD
FD
RFM
FP
RFP
RFSP
MP
MSM
MM
FST
PFP
PFM
D
FP
PF
MP
E
FP
MP
F
RFSP
RFP
FM
FSD
FD
FSM
FP
MST
MP
MSM
MM
G
FP
MP
rlpc

PLATE 155. Melanoblossiinae Roewer, 1933, *Melanoblossia braunsi* Purcell, 1903, chelicerae, prolateral (**A, B**), retrolateral (**C, D, F, G**), and retroventral (**E**) views, illustrating dentition, setae, and *type C sfc*. **A–E.** ♂ (AMNH [LP 10737]), with (**A**) and without (**B**) *sfc* illustrated, with cheliceral fingers open (**C**) and closed (**D**), and illustrating positions of fondal teeth relative to median series (**E**). Numbers indicate seven distalmost toothlike structures. **F, G.** ♀ (AMNH [LP 10737]), illustrating abnormal bifid tooth (arrow). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **MST,** movable finger, subterminal teeth (denticles); ***pdp*,** prodorsal proximal setae; **PF,** profondal teeth; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal teeth; ***rlpc*,** retrolateral proximal setal cluster; ***sfc*,** setiform flagellar complex.

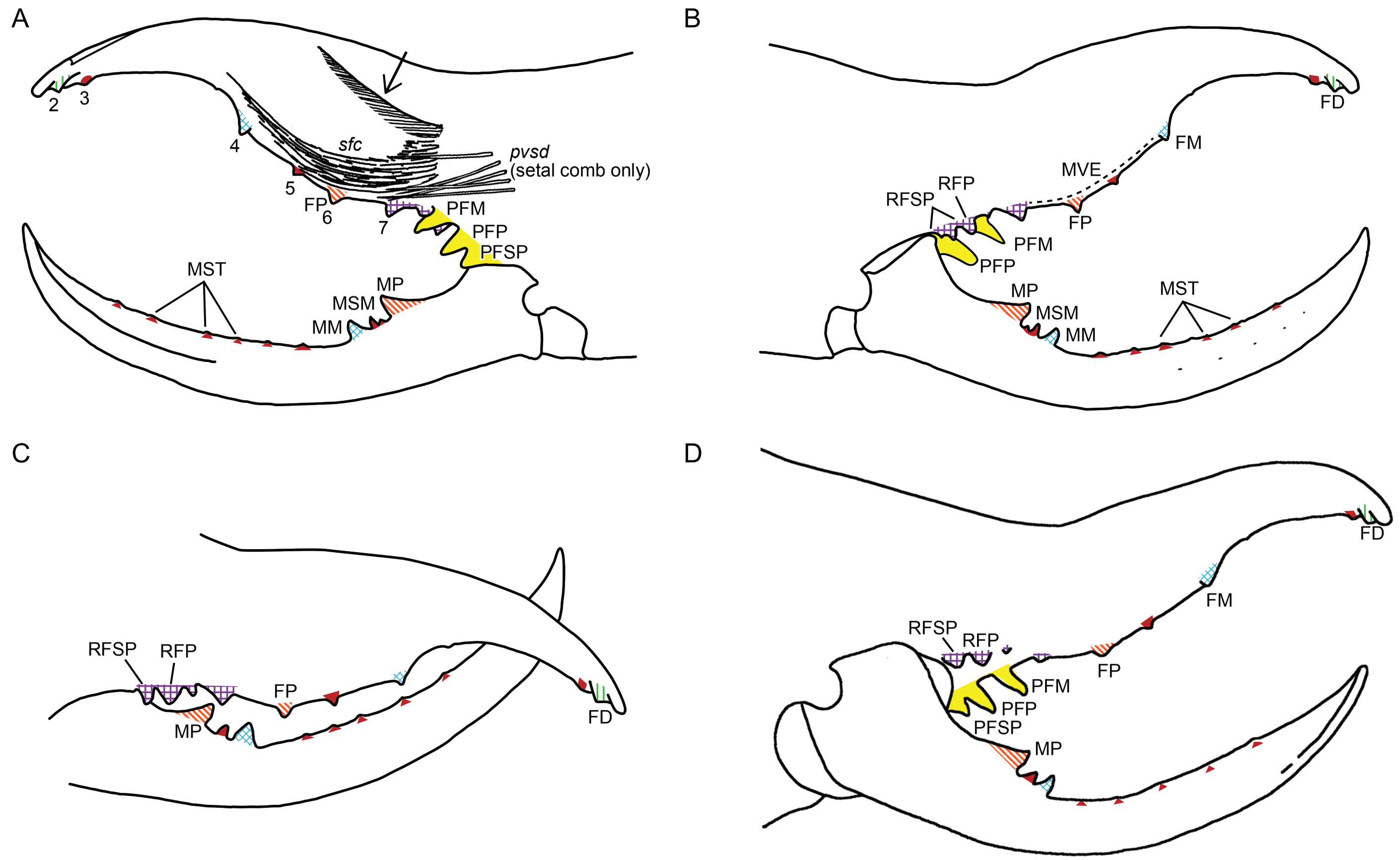

A
2
3
4
sfc
pvsd
(setal comb only)
5
FP
6
7
PFM
PFP
PFSP
MST
MP
MSM
MM
B
FD
FM
MVE
RFP
RFSP
FP
PFM
PFP
MP
MSM
MM
MST
C
RFSP
RFP
FP
MP
FD
D
FD
FM
RFSP
RFP
FP
PFM
PFP
PFSP
MP

PLATE 156. Melanoblossiinae Roewer, 1933, *Melanoblossia* cf. *braunsi*, ♂ (AMNH [LP 8550]), chelicerae, prolateral (**A**), retrolateral (**B, C**), and retroventral (**D**) views, illustrating dentition, setae, and *type C sfc* with cheliceral fingers open (**A, B**), closed (**C**), and illustrating fondal teeth (**D**). Arrow indicates *sfc principal seta*. Numbers indicate seven distalmost toothlike structures. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **MST,** movable finger, subterminal tooth; **MVE,** medioventral excrescence; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth; ***sfc*,** setiform flagellar complex.

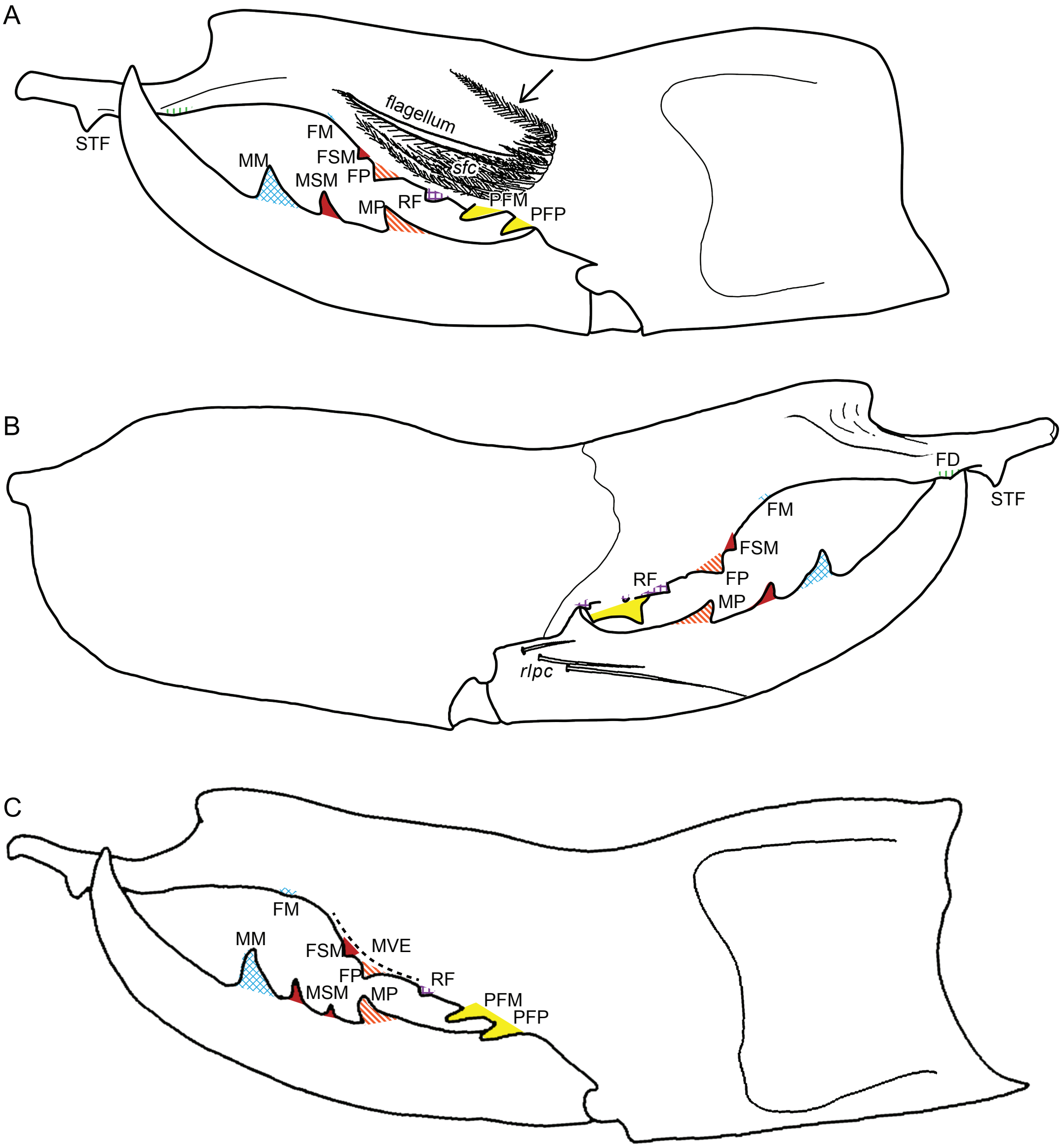

A
flagellum
sfc
STF
FM
FSM
MM
MSM
FP
MP
RF
PFM
PFP
B
FD
STF
FM
FSM
RF
FP
MP
rlpc
C
FM
MM
FSM
MVE
FP
RF
MSM
MP
PFM
PFP

PLATE 157. Melanoblossiinae Roewer, 1933, chelicerae, prolateral (**A, C**) and retrolateral (**B**) views, illustrating *type C sfc*, and population variation in MSM teeth. **A–C.** *Melanoblossia* sp. **A, B.** ♂ (AMNH [LP 9857]). **C.** ♂ (NMNW 13396). Arrow indicates *sfc principal seta*. Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSM,** fixed finger, submedial tooth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial tooth; **MVE,** medioventral excrescence; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **RF,** retrofondal teeth; ***rlpc*,** retrolateral proximal setal cluster; ***sfc*,** setiform flagellar complex; **STF,** subterminal flange.

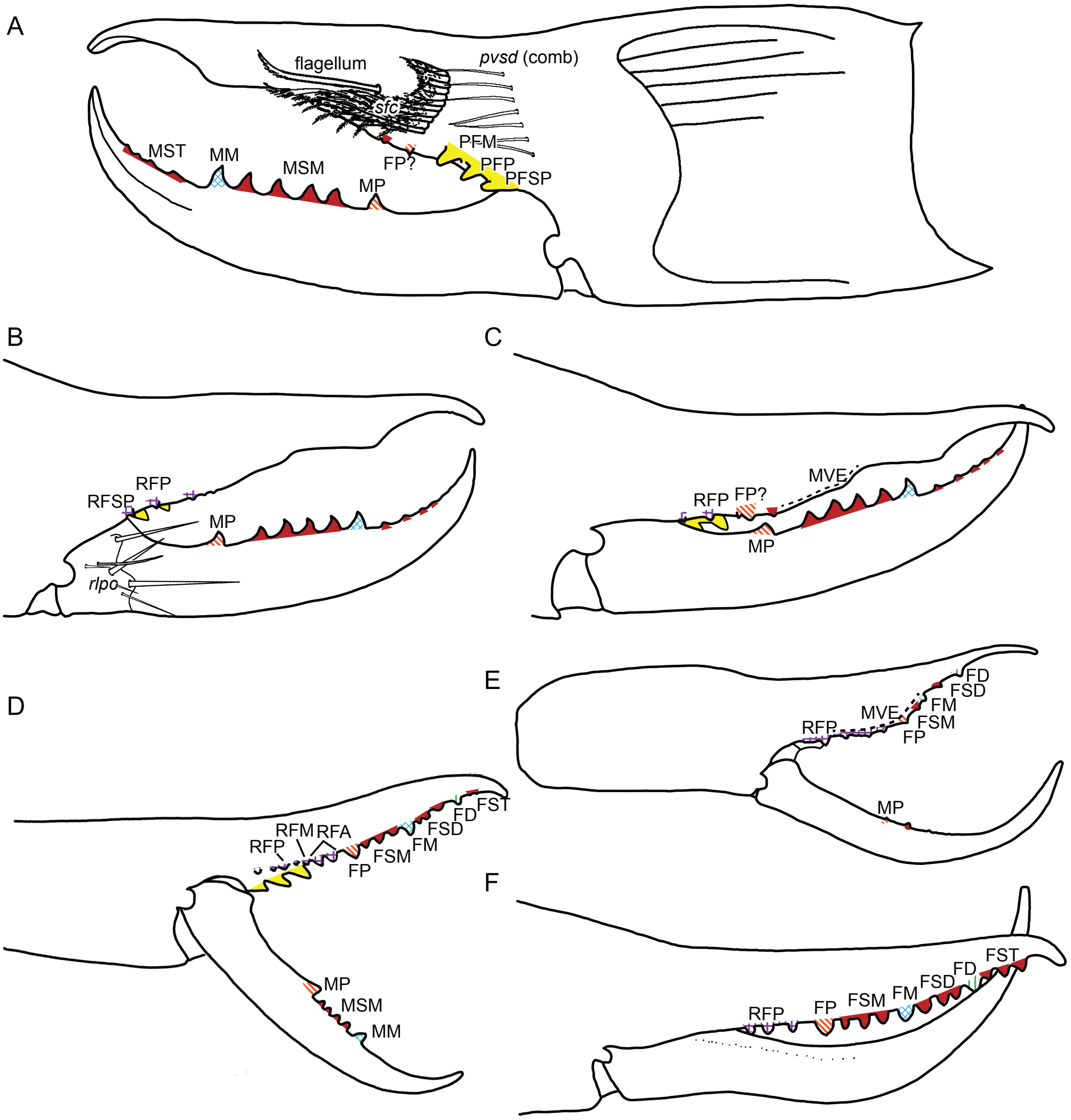

A
flagellum
pvsd (comb)
sfc
MST
MM
MSM
MP
FP?
PFM
PFP
PFSP
B
RFP
RFSP
MP
rlpc
C
MVE
RFP
FP?
MP
D
RFM
RFA
RFP
FP
FSM
FM
FSD
FD
FST
MP
MSM
MM
E
FD
FSD
FM
MVE
RFP
FSM
FP
MP
F
FST
FD
FSD
FM
FSM
FP
RFP

PLATE 158. Melanoblossiinae Roewer, 1933, chelicerae, prolateral (**A**), retrolateral (**B, C, E, F**), and retroventral (**D**) views, illustrating dentition, setae, and *type C sfc*. **A–C.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). **D.** *Lawrencega tripilosa* Lawrence, 1968, ♀ (NMNW 11118). **E, F.** *Lawrencega minuta* Wharton, 1981. **E.** Paratype ♂ (CAS 9033898), flagellar complex not illustrated. **F.** Paratype ♀ (CAS 9033898). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal teeth; **FSM,** fixed finger, submedial teeth; **FST,** fixed finger, subterminal teeth; **MM,** movable finger, medial tooth; **MP,** movable finger, proximal tooth; **MSM,** movable finger, submedial teeth; **MST,** movable finger, subterminal tooth; **MVE,** medioventral excrescence; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; ***pvsd*,** proventral subdistal setae (setal comb only); **RFA,** retrofondal apical tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSP,** retrofondal subproximal tooth; ***rlpc*,** retrolateral proximal setal cluster; ***sfc*,** setiform flagellar complex.

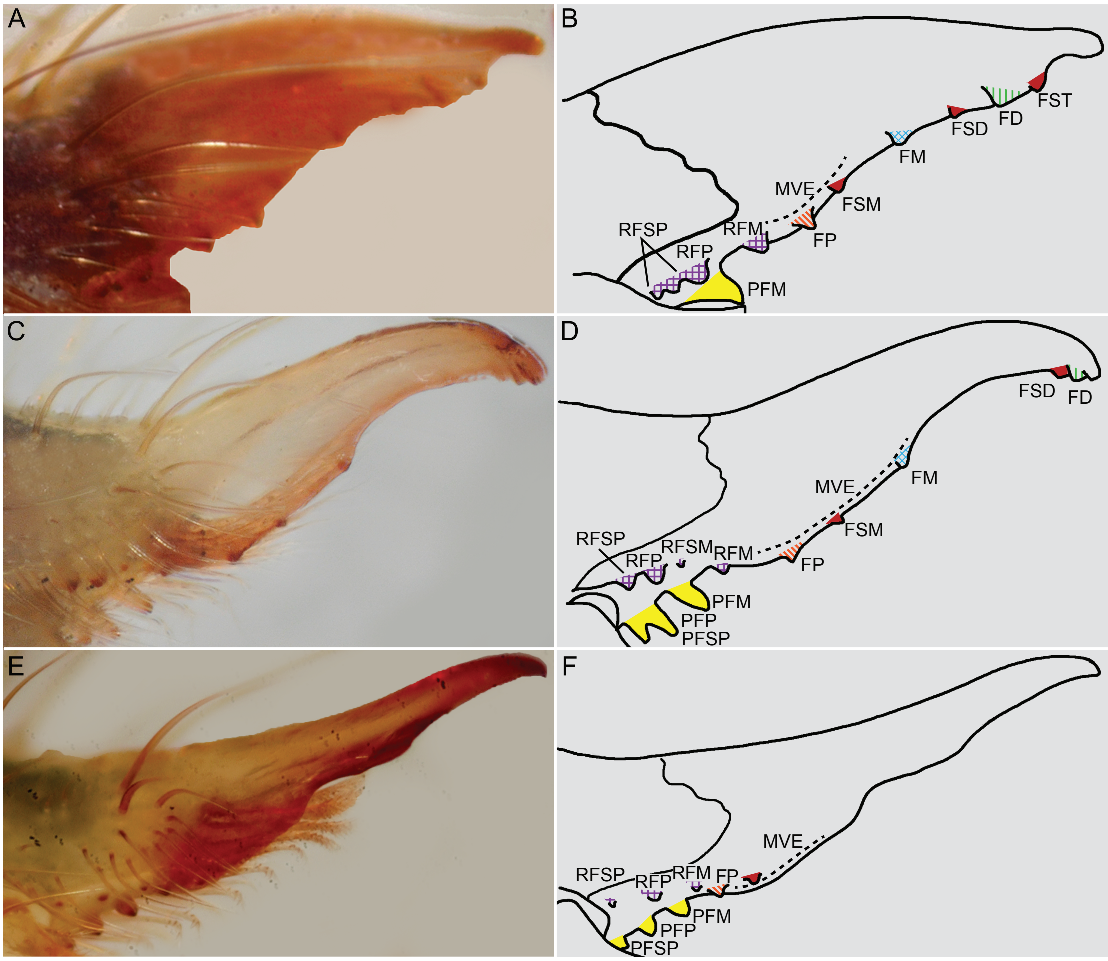

A
B
FST
FD
FSD
FM
MVE
FSM
RFSP
RFM
RFP
FP
PFM
C
D
FSD
FD
FM
MVE
FSM
RFSP
RFSM
RFP
RFM
FP
PFM
PFP
PFSP
E
F
MVE
RFSP
RFP
RFM
FP
PFM
PFP
PFSP

PLATE 159. Melanoblossiinae Roewer, 1933, cheliceral fixed fingers, retroventral views illustrating fondal area. **A, B.** *Melanoblossia braunsi*, Purcell, 1903, ♂ (AMNH [LP 10737]). **C, D.** *Melanoblossia* cf. *braunsi*, ♂ (AMNH [LP 8550]). **E, F.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). Abbreviations: **FD,** fixed finger, distal tooth; **FM,** fixed finger, medial tooth; **FP,** fixed finger, proximal tooth; **FSD,** fixed finger, subdistal tooth; **FSM,** fixed finger, submedial tooth; **FST,** fixed finger, subterminal tooth; **MVE,** medioventral excrescence; **PFM,** profondal medial tooth; **PFP,** profondal proximal tooth; **PFSP,** profondal subproximal tooth; **RFM,** retrofondal medial tooth; **RFP,** retrofondal proximal tooth; **RFSM,** retrofondal submedial tooth; **RFSP,** retrofondal subproximal teeth.